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AN ECOLOGICAL STUDY OF THE DOUGLAS FIR VEGETATION IN BANFF AND JASPER NATIONAL PARKS

by

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A THESIS

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The undersigned certify that they have read and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled, "AN ECOLOGICAL STUDY OF THE DOUGLAS FIR VEGETATION IN BANFF AND JASPER NATIONAL PARKS", submitted by Paul William Stringer, in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

The floristic composition and vegetation structure of the mature phase of the Douglas fir ecosystem in Banff and Jasper National Parks were studied, and data obtained on physical environmental factors operative on the primary producer level of this ecosystem.

Twenty stands of uniform, mature, undisturbed Douglas fir (*Pseudotsuga menziesii* var. *glauca*) forest were selected using aerial photographs and visual inspection. Restricted random sampling methods and nested quadrats were used to quantitatively estimate structural attributes of all strata, as well as selected edaphic and topographic factors.

One hundred and forty vascular species were recorded, only fifteen having Presence values over 80% and only twelve having mean quadrat Frequencies over 20%. Scattered mature trees of *Pinus contorta* occurred within the Douglas fir forest, as well as sporadic clumps of *Picea glauca*, *Populus tremuloides* and young *Pinus contorta*. Species prominent in the poorly developed shrub stratum were *Shepherdia canadensis*, *Rosa acicularis*, *Spiraea lucida* and *Juniperus communis*. The more prominent herb and dwarf shrub, bryophyte and lichen species were *Elymus innovatus*, *Arctostaphylos uva-ursi*, *Calamagrostis rubescens*, *Fragaria virginiana*, *Astragalus decumbens*, *Aster conspicuus*, *Linnaea borealis*, *Hylocomium splendens*, *Abietinella abietina*, *Tortula ruralis* and *Peltigera canina*.

Multiple regression analysis was used to investigate the relationship between the vegetation structure and environment, using attributes of the tree and understory strata as dependent variables, and selected edaphic, topo-

graphic and vegetation attributes as independent variables. Available potassium and phosphorus, slope aspect and effective stand age were most influential in tree stratum development. Understory strata were primarily dependent on attributes of the tree stratum but the herb and dwarf shrub stratum was especially correlated with the presence of *Pinus contorta*.

A two-dimensional ordination was constructed based on the floristic similarity of the vascular understory vegetation of stands. A strong floristic discontinuity between Banff and Jasper was thought to be primarily caused by attributes of the tree stratum pertaining to stand history, although macroclimate, elevation, soil free lime content and moisture characteristics all probably had some influence. The floristic discontinuity prompted recognition of two associations: *Pseudotsuga/Elymus innovatus* association in stands at Jasper and *Pseudotsuga/Arctostaphylos uva-ursi - Calamagrostis rubescens* association in stands at Banff. The latter association was found in young, discontinuous-canopied stands containing a relatively high proportion of *Pinus contorta*, whereas the *Pseudotsuga/Elymus* association was found in mature, closed-canopy stands. It was suggested that these two associations represent different stages in a maturity cycle of Douglas fir forest. *Pinus contorta* decreased in importance as the forest matured and became locally dominant due to fire disturbance.

Close similarity was found between the floristic composition of the Banff and Jasper ecosystems and other Douglas fir forests in southern British Columbia and western Montana.

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I INTRODUCTION

Douglas fir was discovered by Archibald Menzies, the surgeon of Captain Vancouver, at Nootka Sound on Vancouver Island in 1797. Another collection was made by Meriwether Lewis on the banks of the Columbia River in 1805-6, and from that same region David Douglas in 1827 collected cones and other material and sent them back to Europe to the Horticultural Society of London. At various times since 1827, eighteen different names have been given to this species based on these three collections (Krajina, 1956). The first generally accepted name was *Pseudotsuga mucronata* (Raf.) Sudw., but since the early part of this century up to 1950 the accepted name has been *Pseudotsuga taxifolia* (Poir.) Britton. In 1950, J. Do Amaral Franco showed that this name should be rejected as it was a later homonym of *Abies taxifolia* (Desf.) (1804). Franco proposed the new combination based on the next oldest name *Pseudotsuga menziesii* (Mirb.) Franco based on A. *menziesii* Mirb. 1825 which had been previously overlooked (Little, 1953).

There are four other species of *Pseudotsuga*, only one of which is native to North America (*Pseudotsuga macrocarpa* Mayr., the large-coned Douglas fir or bigcone spruce). The other three species are native to southeast Asia: *P. sinensis* Dode. in western China, *P.*

wilsoniana Hayata in S.W. China and Taiwan and *P. japonica* (Shirasawa) Beissner in S.E. Japan (Dallimore and Jackson, 1948, pp. 582, 585 and 592). *Pseudotsuga macrocarpa* is found on steep rocky slopes in the mountains of southern California from the Santa Inez Mtns. to the southern border of California. It is easily distinguished from *P. menziesii* by its large cones which are 3½ - 7 inches long and 2 - 2½ inches wide (Dallimore and Jackson, 1948, p. 584).

Varieties of Douglas Fir (*P. menziesii*)

It is now accepted that two varieties of this species can be distinguished as follows.

Pseudotsuga menziesii var. *menziesii* (Mirb.) Franco, the Coast or Oregon Douglas fir, occurs west of the Cascade and Coast Ranges in Washington, Oregon and British Columbia, and west of the Sierra Nevada in northern California (U.S.D.A. For. Ser. 1965, p. 547).

Pseudotsuga menziesii var. *glauca* (Beissn.) Franco, the Blue, Colorado or Rocky Mountain Douglas fir occurs on the east slopes of the Cascade, Coast Ranges and the Sierra Nevada, and along the whole range of the Rocky Mountains from central Mexico to central British Columbia and Alberta. Its range overlaps with that of var. *menziesii* only in south British Columbia and northeastern Washington (U.S.D.A. For. Ser. 1965, p. 554).

The major differences between these two varieties

are in morphology, growth rate and environmental requirements, summarized as follows (Little, 1952; Dallimore and Jackson, 1948, pp. 581 and 586).

Var. *glauca* has thickened, blue-green leaves with an odour of turpentine, and pubescent or glabrous twigs. Cones are 4 to 7 cm long with reflexed or sometimes erect, exserted three-lobed bracts. It has resinous winter buds.

Var. *menziesii* has thinner, dark yellow-green leaves with an odour of pineapple, and pubescent twigs. Cones are 6 to 10 cm long with erect, exserted, three-lobed bracts. It has non-resinous winter buds.

Var. *glauca* is much the slower-growing tree and is smaller in height than var. *menziesii*, rarely reaching 150 feet.

Var. *menziesii* usually exceeds 220 feet in height at maturity and may reach 300 feet.

Var. *glauca* is considered the hardier variety as it is adapted to a more severe, drier climate of greater temperature extremes. It is less liable to injury by spring frosts. The mean annual precipitation within the range of var. *glauca* is 14 to 45 inches, and 38 to 128 inches within the range of var. *menziesii* (U.S.D.A. For. Ser. 1965, pp. 548 and 554).

Plate 1 Stand 9, July 1965; a Douglas fir (50 - 100 years old) on semi-open, south-facing slope showing typical growth form of medium aged fir.

Distribution

Blue Douglas fir is one of the two major dominant tree species of the montane zone in the Rocky Mountains, the other being the ponderosa pine (*Pinus ponderosa* Dougl.) (Oosting, 1956, p. 296).

It frequently forms pure or nearly pure stands over much of this area within definite altitudinal limits imposed by the variation in environmental factors.

The montane zone merges into the subalpine zone, dominated by *Picea engelmannii* Parry and *Abies lasiocarpa*[1] at its upper altitudinal limit, and into the juniper-pinyon zone dominated by species of *Juniperus* and *Pinus cembroides* Zucc. at its lower altitudinal limits (Daubenmire, 1943a).

The montane zone is considered to be composed of two major climaxes, one dominated by ponderosa pine and the other by Douglas fir, the fir usually forming a distinct sub-zone above the pine (Oosting, 1956, pp. 296 and 301).

The factors determining the boundary between the

---

[1] The complete names of all species recorded in stands at Banff, Jasper and Waterton National Park are listed in Appendix 4 (p. 269) for vascular species and Appendix 5 (p. 281) for bryophytes and lichens. Plant species with complete names in the text have not been recorded in this study.

Douglas fir and the ponderosa pine sub-zones have been the cause of some dispute. Bates (1923) was convinced that the major factor involved was the heat tolerances of the tree seedlings. He suggested that Douglas fir seedlings were more sensitive to high soil temperature than the ponderosa pine; as maximum soil temperature in summer becomes higher down slope, a point is reached at which pine seedlings survive but fir suffer heat injury at the stem base and die.

Daubenmire (1943b) maintained that soil drought was the critical factor involved. He showed that the shading of fir seedlings from excessive insolation did not increase their chances of survival below the normal altitudinal limit. He also found no significant difference between the pine and fir regarding their maximum tolerance to soil temperatures.

In all forest zones in the Rocky Mountains, soil moisture content is favourable in spring and early summer when seedlings germinate, but it decreases progressively throughout the drier summer. Growth water remains available to seedlings just as long as their root systems keep up with the downward retreat of available soil moisture. The species that are most tolerant to dry soil tend to have the greatest rates of root elongation (Daubenmire 1943a).

McMinn (1952) conducted experiments in Idaho and showed that the permanent wilting percentage at a fixed

soil depth was reached progressively later in the year with increasing altitude. This agreed with his observations that ponderosa pine roots do grow faster and penetrate deeper than those of Douglas fir, although both trees have deep taproots. In this respect, ponderosa pine and Douglas fir are far better adapted for successful growth at lower altitudes than the shallow-rooted Engelmann spruce and subalpine fir of the subalpine zone.

It is probable that a combination of soil drought and soil temperature is actually operative; it is extremely difficult to separate the drying effects of high temperature levels, from injury caused to protoplasm by temperature (Daubenmire, 1943a).

The upper limits of the Douglas fir sub-zone are determined by a number of factors, of which temperature and competition appear the more important (Daubenmire, 1943a). At its upper limits, fir is confined to the warmest parts of the topography such as ridge tops and south-facing slopes. Logging or fire, with subsequent higher local temperatures in the closed area, sometimes permit fir establishment in the subalpine zone. However such temporary invasions may result from relaxation of competition rather than from higher temperatures.

Successively higher forest zones in the Rocky Mountains are characterized by dominants of increasing ability to endure shade (Pearson, 1931). Ponderosa pine is less tolerant of shade than Douglas fir, which is in

its turn less tolerant than the Engelmann spruce or subalpine fir in the zone above it. However Pearson (1931) proved, by means of transplant experiments, that seedlings of many of these tree species died above their normal altitudinal limits regardless of the shade factor, so that competitive exclusion probably only applies in intrazonal areas.

Two other factors may influence the distribution of Douglas fir on mountain slopes: soil aeration and ecological succession.

Douglas fir requires a well-aerated soil of not-too-fine a texture. Natural erosion washes fine materials downslope and deposits them at the valley bottoms. Consequently basal slopes tend to have fine, close-packed soils unsuitable for Douglas fir seedling establishment (Daubenmire, 1943a). Soil compaction by the trampling of animals and man may also increase the unsuitability of soils for Douglas fir seedling establishment.

Another factor of importance is succession. The blue Douglas fir, unlike the coast Douglas fir, is generally regarded as a climax species within the montane zone. It may be replaced temporarily or semi-permanently by seral species such as aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta* var. *latifolia*). Such replacement usually results from fire as these two species regenerate on burnt-over areas much more successfully than fir;

lodgepole pine has serotinous cones and aspen regenerates from root sprouts. The fir will not flourish under heavy shade and may be kept out of burn areas by a dense cover of these species (Daubenmire, 1943a).

Progressing northwards, the elevational limits of the Douglas fir sub-zone decrease gradually until the upper limits drop below the elevation of the basal plain in central British Columbia and Alberta.

In the southern Rocky Mountains, the altitudinal limits of Douglas fir are variously given as 7000 - 9000 feet in New Mexico (Bailey, 1913), 7000 feet to the maximum height of the Santa Catalina mountains in Arizona (Shreve, 1915) and 8000 - 9500 feet in Arizona and New Mexico (Pearson, 1931). The most important associated tree species are blue spruce (*Picea pungens* Engelm.), white fir (*Abies concolor* Lindl. & Gord.) and limber pine (*Pinus flexilis* James) in the more exposed habitats (Daubenmire, 1943a). Limber pine and aspen are also named as associates by Pearson (1931).

In the central Rocky Mountains, the altitudinal limits of Douglas fir are given as 6500 - 9000 feet in the Pikes Peak region of Colorado (Whitfield, 1933) and 5600 - 9000 feet in Colorado (Cary, 1911, pp. 218-219), with the more extensive fir forest occurring on the more sheltered north-east facing slopes. Associated tree species of relatively low abundance, are limber pine, white fir and blue spruce above 8000 feet, as well as ponderosa pine

(Whitfield, 1933). The species lists of dominant understory herbs and shrubs listed by the aforementioned authors for the southern and central Rockies differ so widely that understory species can be assumed to be of only local importance. It appears that no species are predominant in the understory over the entire geographic range of blue Douglas fir forest in this region.

Larsen (1930) in an extensive study of vegetational zonation in the northern Rocky Mountains of the United States, gave the following altitudinal limits for the Douglas fir sub-zone:

(1) between 5500 and 9500 feet and generally on southwest slopes and the drier sites, especially at the higher elevations on the eastern slopes of the Rockies;

(2) between 3000 and 5500 feet in western Montana;

(3) between 1000 and 4000 feet in eastern Washington and Idaho.

He was of the opinion that these altitudinal limits were determined chiefly by temperature and precipitation, with higher altitude paralleled by increasing moisture availability and increasingly cooler temperatures. Major climatic differences between these three regions result in the great variation in the altitudinal limits.

In eastern Washington and Idaho, there are relatively mild winters with heavy snowfall and warm dry

summers. Here Douglas fir is associated with ponderosa and lodgepole pine and western larch (*Larix occidentalis* Nutt.) (Larsen, 1930). In some very arid parts of the region, fir is confined to north-facing slopes, protected from the prevalent severe winds (Gail, 1921).

In the Palouse Range of northern Idaho, Douglas fir, together with ponderosa pine, is usually prominent on south-facing slopes. Grand fir (*Abies grandis* (Dougl.) Lindl.), and western red cedar (*Thuja plicata* D. Don) are more prominent on north-facing slopes and in moist ravines at the same elevation as well as in a zone above the fir (Parker, 1952).

In the Flathead and Bitterroot valleys of western Montana, Douglas fir occurs in a "Douglas fir - Western Larch" zone where larch is considered to be a seral species maintained by its greater tolerance to fire than fir, the climax tree of this zone (Larsen, 1930).

Winters are much colder on the eastern slopes of the Rockies, with lighter snowfall and somewhat higher summer rainfall than the other two regions. Lodgepole pine is the most common associate of Douglas fir (Larsen, 1930), but limber pine and white bark pine (*Pinus albicaulis* Engelm.) occur with it on dry rocky ridges (Oosting, 1956, p. 301).

In southern and central British Columbia, Douglas fir is the primary dominant of the tree canopy in four climax "associations" (as the term is used by Daubenmire, 1952)

within the montane zone. The associations are distinguished by different understory dominants, topographic location and soil texture (Brayshaw, 1965):

(1) *Pseudotsuga menziesii - Pinus ponderosa - Arctostaphylos uva-ursi* association, between 2000 and 4000 feet on the gravels and sands of outwash terraces or stony tills,

(2) *Pseudotsuga menziesii - Arctostaphylos uva-ursi - Calamagrostis rubescens* association, between 2500 and 4000 feet on coarse to medium textured soils,

(3) *Pseudotsuga menziesii - Calamagrostis rubescens* association, between 2800 and 4300 feet on medium to fine textured soils,

(4) *Pseudotsuga menziesii - Symphoricarpos albus* association, between 1500 and 3000 feet in ravines and on moist slopes.

Tisdale and McLean (1957) state that *Pseudotsuga/ Calamagrostis* is the most important and widespread association in the Douglas fir part of the montane zone in southern British Columbia; this association also occurs in eastern Washington and northern Idaho (Daubenmire, 1952). Almost pure stands of Douglas fir do occur there, but due to fire, large areas are occupied by lodgepole pine and aspen. Douglas fir occurs in the upper Columbia River valley between the valley floor and 3500 feet, and areas where it is dominant have been divided into two "sub-zones" by McLean

and Holland (1958) as follows.

"Douglas fir groveland" is situated on dry benches and semi-arid lower slopes below 2800 feet, and adjacent to open *Festuca* and *Agropyron* grassland. The only other tree species associated with the fir is *Juniperus scopulorum* Sarg.

"Douglas fir forest" occurs above the groveland at elevations up to 3500 feet, with lodgepole pine and aspen as seral species following logging or fire. Two important associations are recognized by McLean and Holland (1958) in this second sub-zone. The *Pseudotsuga menziesii - Calamagrostis rubescens* association is climax on most of the grey-wooded soils, and the *Pseudotsuga menziesii - Symphoricarpos albus* association is climax on deeper soils and in ravines. These two associations appear identical to two of the four associations given by Brayshaw (1965) as characteristic of the Douglas fir zone. White spruce was reported to be prevalent along river benches in the upper part of the sub-zone.

In Alberta, Douglas fir occurs commonly in three fairly small areas on the east slopes of the Rockies (Rowe, 1959):

(1) Porcupine Hills and Waterton Lakes district;

(2) Bow and Kananaskis River valleys west of Calgary and around Banff townsite;

(3) the Athabasca and Miette River valleys around Jasper townsite.

It also occurs sporadically in the foothills west of Nordegg, in the North Saskatchewan River valley in and near Banff National Park, and at various sites scattered in southwestern Alberta. The northern recorded limit of its range in Alberta is near Brûle Lake (53°15' N, 117°50' W).

Within these areas, Douglas fir is generally confined to warm, dry, south-facing slopes with white spruce more prevalent on north-facing slopes and ravine bottoms. The fir is sometimes accompanied by limber pine on rocky outcrops and stony soils (Rowe, 1959), but its more common associate is lodgepole pine.

Moss (1944) states that the Douglas fir in southwestern Alberta is found with limber pine on rocky ridge-like outliers of the mountains in the black soil zone, more frequently occupied by aspen and *Festuca - Danthonia* grassland. It is also associated with white spruce and lodgepole pine on the higher foothills. Dense stands of Douglas fir occur on sheltered east and northeast slopes of ridges 6 to 10 miles west of Pincher Creek in Alberta, and it was suggested by Moss (1944) that fir is unable to endure the effects of strong dessicating westerly winds. In this same locality the fir sometimes forms dense stands with sparse undercover, but more typically the trees are widely-spaced and accompanied by species commonly associated with aspen. Stands dominated by aspen often form a belt below the fir on the gentler lower slopes. According to Moss (1944) the distribution of Douglas fir east of the continental divide indi-

cates that the species entered post-glacial Alberta from the west through passes in the mountains, not from the south along the divide.

Ecological Life History of *Pseudotsuga menziesii* var. *glauca*

(This section is largely paraphrased from U.S.D.A. For. Ser. 1965, pp. 554 - 556).

Reproduction

The minimum seed-bearing age for blue Douglas fir is about 20 years. Like *Picea* and *Abies* species, Douglas fir cones mature, and the seed dispersed in one year. In central Colorado, staminate and ovulate strobili appear between the end of April and the middle of May depending on elevation, and pollen dispersal begins a few days later. The seed-bearing cones ripen by August or September and begin dispersing seeds soon after. The approximate radius of seed dispersal and reproduction from open grown trees on level land is 100 - 200 yards.

Germination and Development

Successful seed germination and seedling development is helped by partial shade and the presence of litter, provided that the litter doesn't prevent the root penetration to moist soil and doesn't absorb light rain showers.

Dark soils and soils blackened by fire may be unfavourable for development because of surface temperature extremes.

The conflicting theories of Bates (1923) and Daubenmire (1943b) regarding optimum conditions for Douglas fir seedling development have already been discussed (p. 6); it is therefore only necessary to restate that soil moisture and soil temperature are important limiting and controlling factors in the development of Douglas fir seedlings.

The germination and development of *Pseudotsuga menziesii* var. *menziesii* have been studied more than those of var. *glauca*. Isaac and Dimock (1958) found that coast Douglas fir seeds germinated on a wide variety of seed beds provided with adequate moisture and proper temperatures, but the young seedlings grew best on well drained, mineral soils with light shade. Well-established seedlings grew best in bright sunlight.

Douglas fir (without distinction of varieties) has been classified as "intermediate" in tolerance to competition and shade (Baker, 1949). Blue Douglas fir is exceeded in shade tolerance only by Engelmann and white spruce, subalpine fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) amongst its associates; it can endure more shade than western larch, ponderosa pine, lodgepole pine, the pinyons, junipers and aspen (Frothingham, 1909; Spurr, 1965, p. 166).

Spurr (1965) defines a "tolerant species" as one that can "survive and prosper under a forest canopy", and

states that several factors contribute to shade tolerance, namely light intensity, soil moisture and to a lesser extent, several other factors. It is the understory habitat viewed as an integrated whole that determines the nature of tolerance and not any single factor.

The root system of coastal Douglas fir was studied intensively by McMinn (1963) on Vancouver Island. He found that the root system of most young firs consists of a single taproot and a few main laterals (more than 45 degrees to the vertical), and subsequent growth by tertiary and quaternary branching. In normal, older trees the main taproot is supplemented by vertical branches from the main laterals, and the prominence of the taproot gradually obscured by a central deep root system. In suppressed trees the taproot remains prominent and a multiplicity of branching doesn't occur. McMinn (1963) considered the aggressive taproot a useful survival characteristic in young trees. However, where the water table is very high or the soil shallow, roots proliferate laterally to form a plate-like system like that of many other tree species not retaining persistent taproots. I do not know how far the results of these studies of McMinn (1963) or Isaac and Dimock (1958) apply to blue Douglas fir.

Size and Age at Maturity

Blue Douglas fir may attain a size of 150 feet in height and 4 feet in diameter. In the northern Rockies it reaches an average maximum height of 100 - 120 feet with

diameters from 15 - 30 inches in 200 to 300 years; ages rarely exceed 400 years.

Mycorrhizal Associates

Trappe (1962) lists 49 species of fungi from 21 genera as mycorrhizal associates of Douglas fir. He names *Cenococcum gramiforme* (Sow.) Ferd. and Winge, of the Fungi Imperfecti, as of particularly wide occurrence in fir populations. Harley (1959, p. 50) states that *Cenococcum gramiforme* is the most unspecific of all mycorrhizal fungi of forest trees; it has been found on many species of the genera *Pseudotsuga*, *Pinus*, *Picea*, *Juniperus*, *Betula*, *Salix* and *Populus*. It is also widespread in soil even when no hosts are present. Trappe (1965) has investigated the mycorrhizae of both varieties of Douglas fir in California, Oregon, Washington and British Columbia. An unnamed tuberculate mycorrhiza formed by two fungi in combination was found to be common in coastal and blue varieties. One fungus was a white basidiomycete which forms an ectotrophic, profusely-branched and compact mycorrhiza. The other was a phycomycete that covered the aggregate of mycorrhizal tips of the first with a dense dark sheath. The two fungi, unnamed by the author, spread together by means of a rhizomorph composed of a core of the white basidiomycete and a sheath of the dark phycomycete. Trappe reported that this mycorrhizal structure was present in all Douglas fir trees studied.

Principal Predators and Parasites

The principal insect predators of blue Douglas fir are the Douglas fir beetle (*Dendroctonus pseudotsugae* Hopk.) and the spruce budworm (*Choristoneura fumiferana* Clem.) both of which have caused high mortality among fir populations in the Rocky Mountains.

Douglas fir beetle is a bark or cambium-boring insect, and normally only attacks felled, injured or weakened trees; during population maxima it sometimes spreads to healthy trees as well (Keen, 1938, p. 155).

Spruce budworm is the larval stage of a moth, and infestations of this defoliating larva may strip entire trees of foliage (Keen, 1938, pp. 102-104).

No reports have been found of infestations of these two insects on Douglas fir in Alberta, although spruce budworm infestations have been reported regularly every year on other tree species in the province (Anon, 1956-1964).

Douglas fir dwarf mistletoe (*Arceuthobium douglasii* Engelm.) is reported as a damaging parasite throughout the range of Douglas fir, but no reports of its presence in Alberta have been found.

A needlecast fungus (*Rhabdocline pseudotsugae* Syd.) is reported to cause losses in young Douglas fir at cyclic intervals (U.S.D.A. For. Ser. 1965, p. 556).

Many trunk and root rot fungi are listed as serious diseases of the coastal Douglas fir, especially Red Ring Rot

(*Fomes pini* Thore.) and Yellow Ring Rot (*Poria weirii* Murr.). However, the only one to be listed as a serious disease in Alberta is Armillaria Root Rot (*Armillaria mellea* (Fr.) Quél.), which has caused serious losses to lodgepole pine and Douglas fir at Waterton townsite in 1962 and has been spasmodically recorded for many other locations in Alberta on different hosts (Anon, 1956-1964). It has been reported as occurring on Douglas fir in Banff Park in 1964 (E. Carleton, Warden Service, Banff National Park; personal communication).

II OBJECTIVES OF STUDY

The principal objectives of the research reported in this thesis were:

i) To describe the floristic composition, vegetation structure and physical habitats of the mature phase of the Douglas fir ecosystem in Banff and Jasper National Parks, Alberta,

ii) To determine the major physical environmental factors operative on the primary producer level of this ecosystem.

It was considered beyond the scope of this study to investigate the detailed climatology and geology of the area, or to study the higher trophic levels in the ecosystem.

To attain the stated objectives it was desirable to obtain data in a quantitative form whenever possible. Only then could vegetation structure and the physical environment be accurately described, or valid comparisons made with other ecosystems.

The first objective necessitated reasonably accurate estimates of the size and dispersion of the populations of plant species inhabiting the ecosystem. For the

structure of the tree stratum, data on standing crop and the pattern of distribution of each species was also required, as well as data on the size and age of representative trees.

To attain the second objective, it was necessary to measure a broad spectrum of potentially influential, topographic and edaphic environmental factors, such as slope angle, aspect and elevation of site, as well as soil structure, composition and moisture characteristics.

It was hoped that these data would make a useful contribution to a long-term, comprehensive ecological study of Banff and Jasper ecosystems being made by the Plant Ecology Laboratory of the Department of Botany, University of Alberta. With this long-range objective in mind, some of the environmental data, though proven inadequate or unnecessary for this study, could be useful for future workers in allied fields of study.

III DESCRIPTION OF STUDY AREAS

Climate

Summaries of the temperature and precipitation records from four meteorological stations within the study areas are given in Tables 1 and 2. These data were obtained from the Climatology Division of the Meteorological Branch, Department of Transport, Toronto.

All four stations are located in the montane zone of Banff and Jasper, not far from sites occupied by the Douglas fir ecosystem. Maps (Fig. 1, 2 and 3) show the positions of these weather stations (except Waterton H.Q. station) in relation to the locations of the stands studied.

Because most of the Douglas fir stands were located on basal mountain slopes or on ridges in the valley bottom, the elevations of the weather stations roughly coincide with the lowest elevation recorded for any stand in the respective parks. Therefore, although the climatological data can be considered applicable to the Douglas fir ecosystem in Banff, Jasper and Waterton National Parks, local topographic variations will tend to make the relationship only approximate. All four stations are situated in the bottom of main valleys and will be more subject to the phenomenon of cold air drainage than most stand sites (Geiger, 1957, p. 205). Thus the weather stations probably have lower minimum daily temperatures.

The climates at Banff, Anthracite (within the Banff

TABLE 1. PRECIPITATION AT FOUR MONTANE METEOROLOGICAL STATIONS IN THE STUDY REGION

Expressed as normals for period of 30 years (1931-60) in inches (Anon 1965).

Station	Annual Precipitation	Annual Rainfall	Annual Snowfall	Highest Monthly Rainfall	Highest Monthly Snowfall	Highest Monthly Precipitation
Anthracite[b]	18.34	11.91	64.3	2.65 June	11.6 Jan.	2.68 June
Banff town	18.48	10.55	79.3	2.41 June	14.0 Dec.	2.45 June
Jasper town	15.98	11.06	49.2	2.15 June	10.9 Dec.	2.15 June
Waterton Park HQ[a]	42.31	19.46	228.5	4.99 June	38.0 Jan.	5.17 June

NOTES: [a] Based on a period of record of 10-24 years during 1931-60

[b] 3 mls east of Banff townsite.

TABLE 2. TEMPERATURES AT FOUR MONTANE METEOROLOGICAL STATIONS IN THE STUDY REGION

Expressed as normals for period of 30 years (1931-60) in ° Fahrenheit (Anon 1964).

Station and Elevation in Feet	Mean Annual	Hottest Month[a]			Coldest Month[a]		
		Mean Daily	Mean Daily Maximum	Mean Daily Minimum	Mean Daily	Mean Daily Maximum	Mean Daily Minimum
Anthracite 4500	36.8	58.6	73.5	43.7	13.4	22.4	4.4
Banff 4538	36.0	58.0	72.5	43.5	12.6	21.7	3.5
Jasper 3472	37.3	59.4	73.6	45.2	11.5	21.0	2.0
Waterton Park HQ[b] 4250	40.9	63.2	75.1	51.2	18.5	27.0	9.9

NOTES: [a] For all four stations the hottest month is July
For all four stations the coldest month is January

[b] Based on a period of less than 10 years, but adjustments have been made when an unusually warm or cold month unduly influenced the average values.

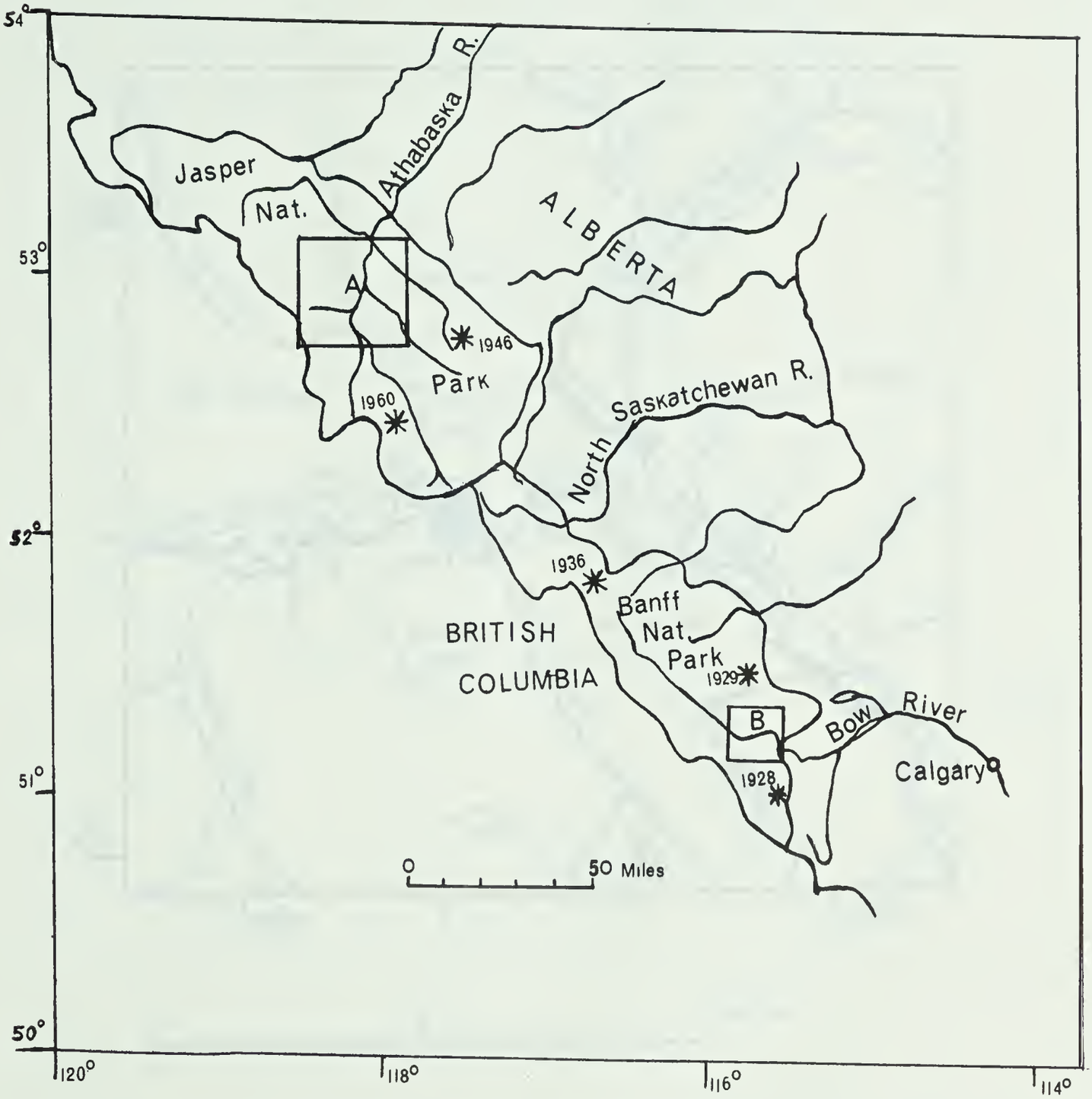


FIGURE 1. LOCATION OF DOUGLAS FIR STUDY AREAS AND MAJOR FOREST FIRES IN BANFF AND JASPER NATIONAL PARKS

* Major Forest Fires

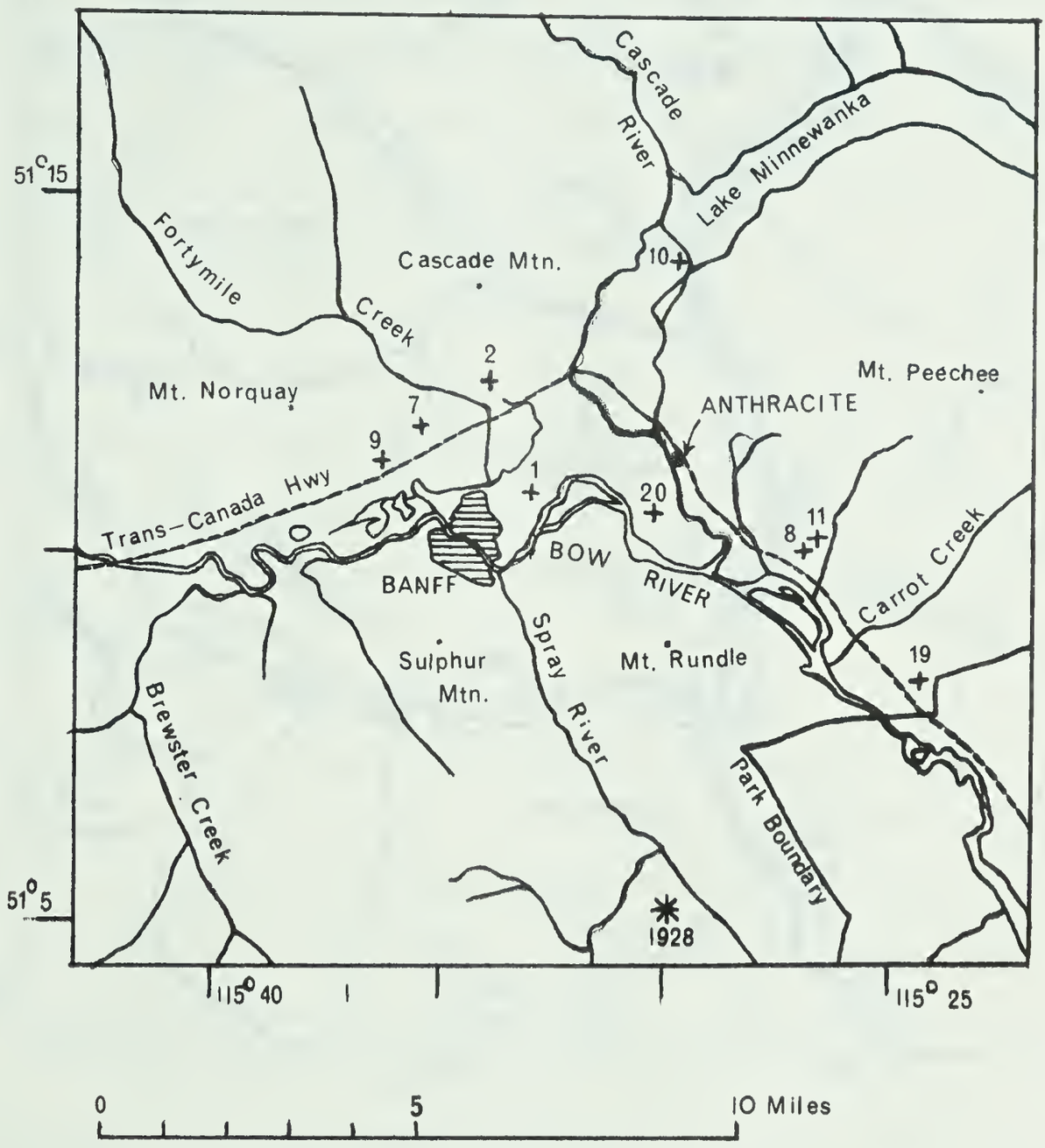


FIGURE 2. LOCATION OF STANDS AND SOME MAJOR FOREST FIRES IN BANFF NATIONAL PARK

(See Insert B in Figure 1)

* Forest Fires

+ Stands

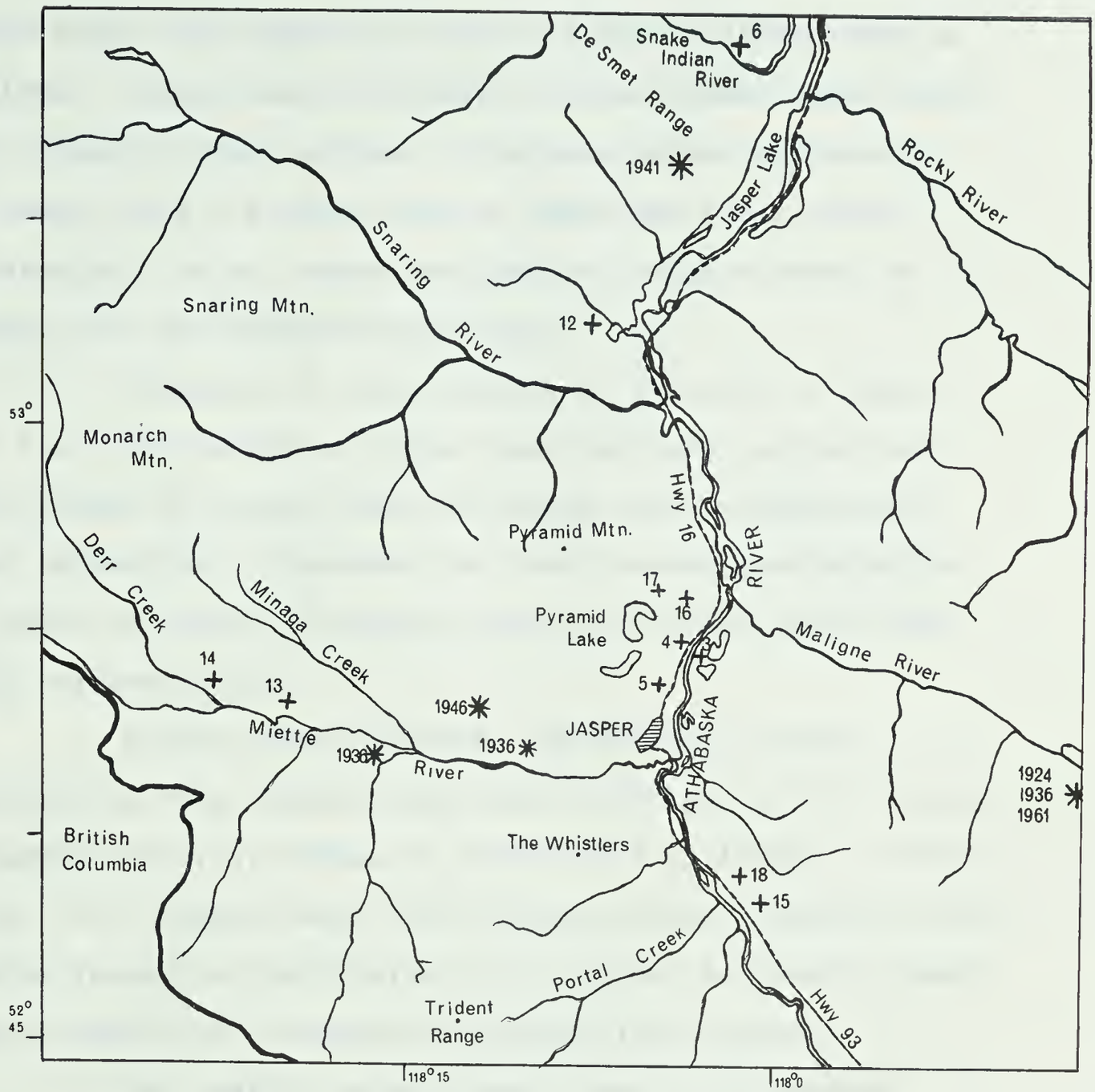


FIGURE 3. LOCATION OF STANDS AND SOME MAJOR FOREST FIRES IN JASPER NATIONAL PARK

(See Insert A in Figure 1)

* Forest Fires

\+ Stands

study area) and Jasper are very similar and differ only as follows. Jasper has fractionally warmer summers than Banff, but slightly colder winters. The mean annual temperature of Jasper is 1.3°F above that of Banff and 0.5°F above Anthracite. At all three stations the coldest month is January and the warmest month July.

Although the total amount of rainfall is similar for the three stations, Jasper has the lowest annual snowfall, about 30 inches less than Banff and 15 inches less than Anthracite. Therefore the total annual precipitation is about 16 inches at Jasper, about 2.5 inches lower than Banff or Anthracite.

At all three stations, the highest rainfall occurred in June, Jasper receiving an average of 2.15 inches, compared with 2.41 inches at Banff and 2.65 inches at Anthracite. In a normal year, the heaviest monthly snowfall occurs during January at Anthracite (11.6 inches) but during December at Banff (14.0 inches) and Jasper (10.9 inches).

One possibly significant climatic difference between the two townsite stations is that Banff tends to receive heavier snowfall in early spring than Jasper. For example, during March and April, the normal Banff snowfall is 8.9 and 10.0 inches respectively, whereas similar figures for Jasper are 5.0 and 2.7 inches. Anthracite is intermediate with 8.0 and 5.9 inches. This differential abundance of moisture for spring growth could result in

differences in the composition and structure of vegetation between the two areas. However, the difference may lose some significance since May and June precipitation is relatively heavy in both areas. The lower spring snowfall at Jasper probably results in the soil surface being exposed sooner than at Banff and a consequent earlier start to the growing season.

An analysis of the water balances of the main valleys of Banff, Jasper and Waterton National Parks was made by calculating potential and actual monthly evapotranspiration and comparing these data with precipitation normals at the four stations (Fig. 4).

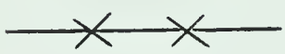
Evapotranspiration was calculated using the method of Thornthwaite (Thornthwaite and Mather, 1957) based on the monthly mean temperature and station latitude. A soil moisture reserve of 4.0 inches was used, as recommended by Sanderson (1948) for most agricultural soils, for want of a more accurate estimate. This soil moisture reserve will vary according to the type of vegetation and the texture and depth of soil, so that quite small variations in topography, soil or vegetation cover will result in a corresponding change in the soil moisture reserve value. It is not known how applicable is the value of 4.0 inches soil moisture reserve to the Douglas fir ecosystem, but it can be assumed that the values are very similar for the Banff, Jasper and Waterton areas and so comparisons are valid.

Potential evapotranspiration at Jasper greatly

FIGURE 4. EVAPOTRANSPIRATION AND PRECIPITATION CHARTS FOR METEOROLOGICAL STATIONS WITHIN BANFF, JASPER AND WATERTON NATIONAL PARKS

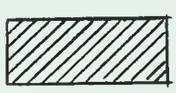
Soil moisture storage taken to be 4 inches (after Sanderson, 1948).

Precipitation in inches



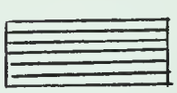
Potential evapotranspiration in inches

Water deficiency



Water surplus

Soil moisture utilization



Soil moisture recharge

4 A Banff

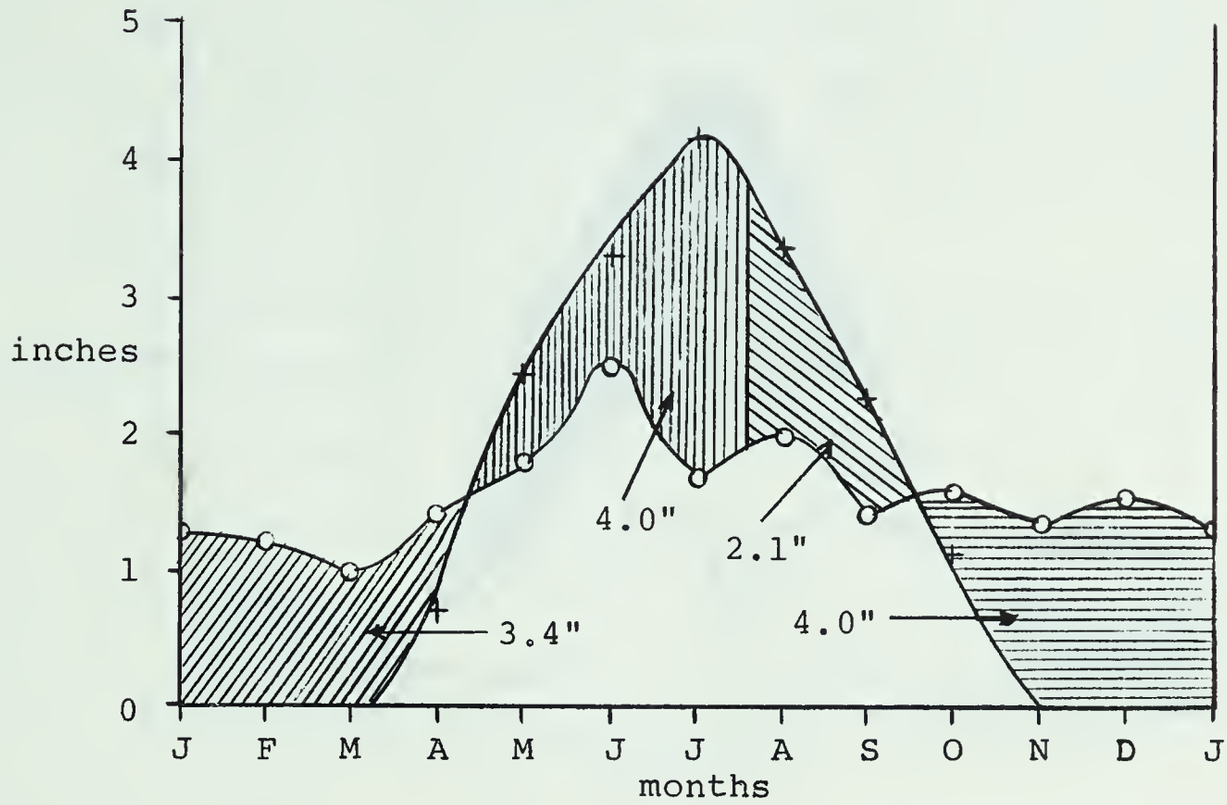
4 B Anthracite

4 C Jasper

4 D Waterton Park H.Q.

FIGURE 4.

A. Banff



B. Anthracite

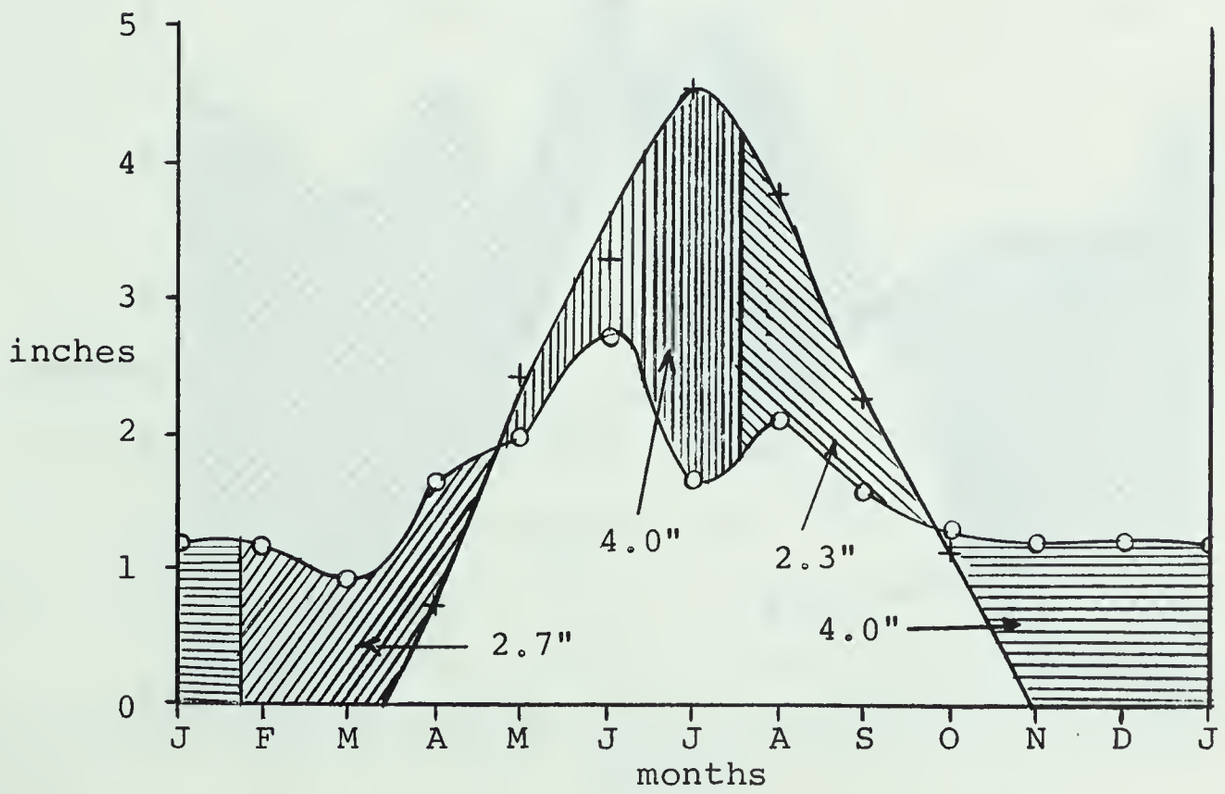
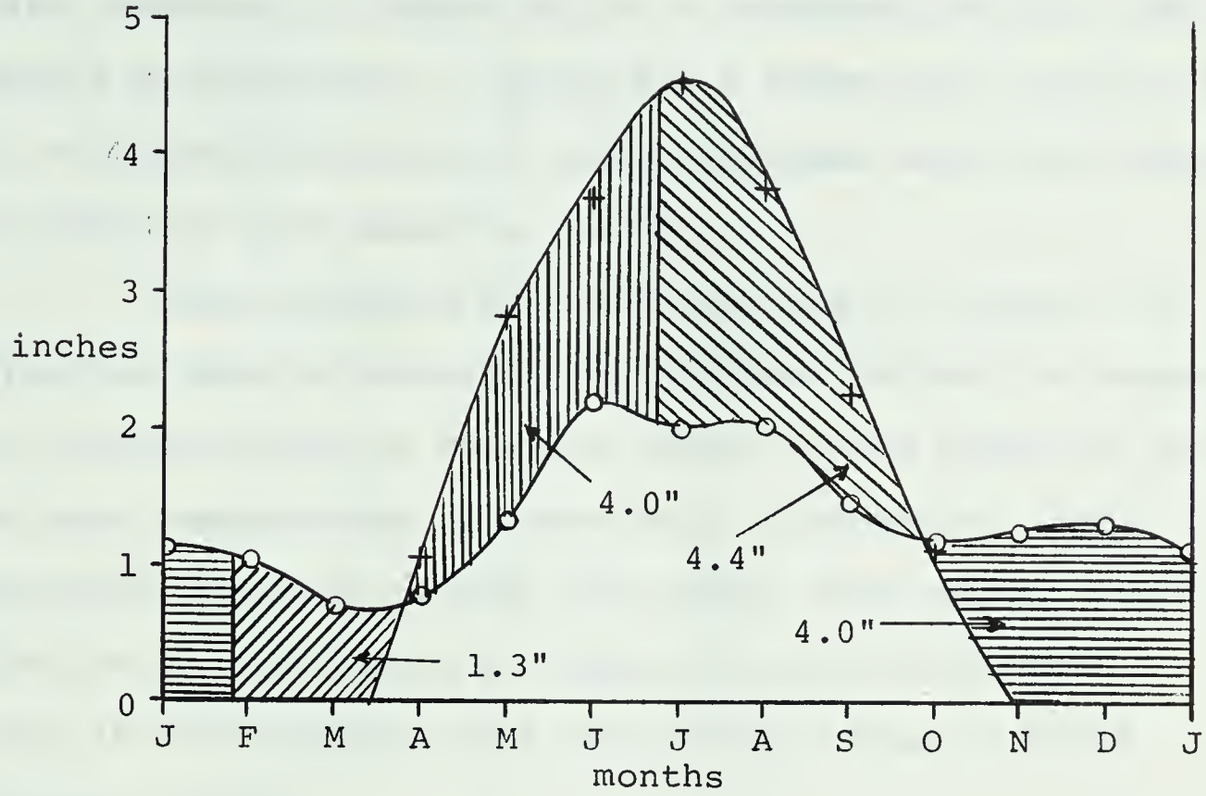
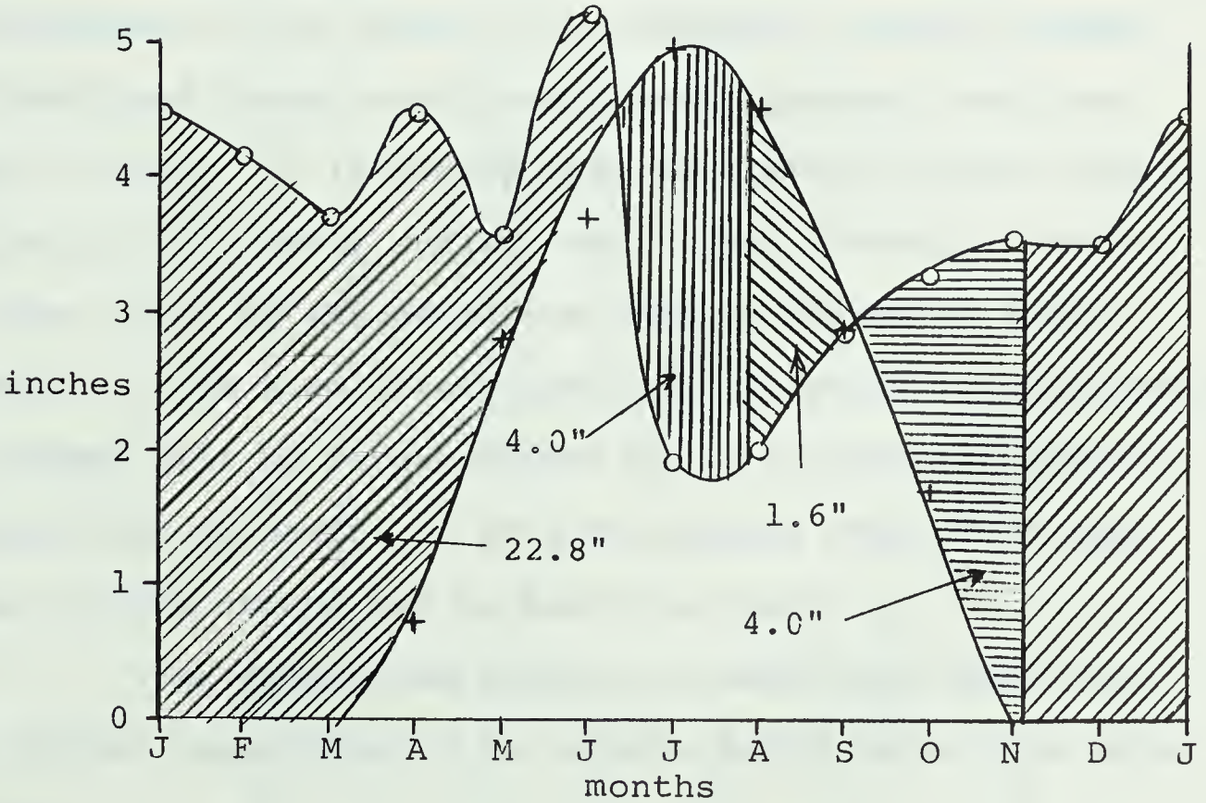


FIGURE 4. (continued)

C. Jasper



D. Waterton Park H.Q.



exceeds precipitation in spring and early summer. Therefore reserve moisture in Jasper soils is exhausted earlier than at Banff or Anthracite. Jasper has a three month period of soil moisture deficiency in summer, whereas Banff and Anthracite deficits last about two months.

These moisture deficits may tend to shorten the "Effective Growing Season" which has been defined on temperature criteria alone by Boughner (1964) as the number of days with mean temperatures of above 42°F, discounting those individual warm days outside the normal warm season. The effective growing season at Jasper is nine days longer (Table 3) and commences four days earlier than at Banff (Boughner, 1964).

Observations in the field indicated that the differences in the onset of the effective growing season in Banff and Jasper were considerably greater than four days in 1965. It is likely that the heavier winter snowfall (especially in early spring) and higher elevation result in a later onset of the effective growing season at Banff. However, it is also likely that the effective growing season at Jasper will be foreshortened by soil moisture deficits sooner than at Banff, so that the period over which most plant growth occurs may be about the same.

The frost-free seasons at Banff and Jasper do not differ significantly in length, Banff being four days longer.

The differences in climate between Banff, Anthra-

TABLE 3. FROST-FREE AND EFFECTIVE GROWING SEASONS AT FOUR MONTANE METEOROLOGICAL STATIONS

Expressed as normals for period of 10 years (1950-59) (Boughner, 1964).

Station	Location of Station	Frost-Free Season	Effective Growing Season
Banff	51°11'N, 115°34'W	June 6 - September 2 88 days	May 5 - September 30 148 days
Jasper	52°53'N, 118°04'W	June 9 - September 1 84 days	May 1 - October 5 157 days
Anthracite	51°11'N, 115°29'W	NA[a]	NA[a]
Waterton Park HQ	49°4'N, 113°57'W	NA[a]	NA[a]

NOTES: [a] NA = Not Available.

cite and Jasper seem insignificant when the Waterton climate is also considered. Waterton has far warmer summers and winters (Table 2), and much higher rainfall in the summer and snowfall in the winter. Unfortunately no data are available on the frost-free period or effective growing season, but the climate of Waterton does appear to be more moist and temperate than that of Banff or Jasper. The late summer period of moisture deficiency is only about one month long due to the heavy precipitation which exceeds potential evapotranspiration right up to the end of June (Fig. 4). The late summer moisture deficiency of 1.6 inches is soon made up in the fall, and then a moisture surplus of 22.8 inches accumulates as snow during the rest of the winter. The precipitation more than compensates for the higher evapotranspiration and results in a much more mesic environment at Waterton.

Geology

The Banff study area, and the two northernmost stands at Jasper (Stands 6J and 12J, Appendix 1, p. 266) are in the east range, whereas most of the Jasper study area is in the main range of the Rocky Mountains (Dr. H.A.K. Charlesworth, Department of Geology, University of Alberta; personal communication).

The east range is a series of thrust sheets exposing Mesozoic shales, sandstones and carbonates, and Paleozoic

carbonates and shales. The main valleys are U-shaped, and the entire floor, except for the floodplain, is covered with a blanket of till and glacio-fluvial deposits. In the Bow Valley the knobs and ridges are composed of bedrock covered with varying thicknesses of glacial drift. East of Banff townsite and above the floodplain of the Bow River, there is an extensive terrace composed of outwash, probably formed after the glaciers had retreated far up their valleys (Rutter, 1965). This terrace also contains large areas of Douglas fir forest. The till and glacio-fluvial outwash deposits are mainly composed of limestone, dolomite and shale with a little quartz sandstone, and are derived from bedrock underlying the Bow River valley system.

The main range consists of a single, complex, Castle Mountain thrust sheet, exposing Precambrian slates and sandstones, Lower Cambrian sandstones and quartzites and Paleozoic carbonates and shales (Dr. H.A.K. Charlesworth, Department of Geology, University of Alberta; personal communication).

Like Banff, the main valleys at Jasper are U-shaped due to glaciation, and much of the Douglas fir vegetation is situated on the basal slopes and ridges in the valley bottoms. These sites may have bedrock exposed at the surface or be covered with a layer of glacial drift of varying thickness. Many ridges paralleling the Athabasca River valley (the main valley in Jasper Park) have sandstones and conglomerates at the surface, unlike the ridges

in the Bow River valley at Banff.

Fire History

Most of this information was abstracted from the records of the Warden Service, National Parks Branch, Department of Northern Affairs and National Resources, and by personal communication with E. Carleton, Warden Service, Banff National Park, and M. McGuire, Chief Warden, Jasper National Park.

Banff National Park was established in 1885 and Jasper National Park in 1907. Fire records were kept only after the installation of a permanent Warden Service in 1909 at Banff and in about 1915 at Jasper; the history of fires in the parks before these dates is therefore scattered and incomplete. However it is evident that fires were of widespread and frequent occurrence prior to establishment of the parks, especially in the main valleys.

Very large areas of even-sized, and probably even-aged lodgepole pine and smaller areas of aspen indicate the extent of these fires, the causes of which included lightning, Indians and early pioneers. Prospectors are reported to have started many fires to aid in uncovering rock strata, and to mark areas for further digging. Fires were very common during the years of railroad construction. The Canadian Pacific Railway tracks were laid through the Bow Valley in Banff from 1883 to 1885; many fires burned

unchecked on the lower mountain slopes caused by sparks produced by the coal-burning locomotives. Flames generally spread down the valley with the prevailing westerly winds and up the mountain slopes, sometimes to timberline. The Canadian National Railway tracks were put through Jasper much later (1910-12); a similar increase in fires may have occurred during this period.

Fire records have been kept in Banff since 1909 when regular fire patrols on trails close to Banff and on hand cars on the railway were initiated. Since that time most fires have been of minor importance, consisting mostly of ground fires in grassland or forest litter, and occurring in areas close to human activity in the main valleys. Major crown fires were reported for the Eau Clair and Goat Mountain areas in 1928, Cuthead Summit in 1929 and the Silverhorn Creek area in 1936 (Figs. 1 and 2).

At Jasper there were no detailed fire reports previous to 1940 but major crown fires were noted in correspondence for the Medicine Lake area in 1924, Caledonia Lake, Medicine Lake and the Miette River valley near Giekie in 1936 and the North Saskatchewan River valley near Nigel Creek in 1938 (just inside Banff National Park). Since 1940, major fires were recorded from the Roche de Smet in 1941, the upper Maligne valley and Minnow Lake in 1946, Morris Creek in 1956, Chaba River in 1960 and Medicine Lake areas in 1961 (Figs. 1 and 3).

It is probable that many areas in the main valleys

at Banff and Jasper have been affected by light ground fires since 1909 and 1915, respectively, but rarely has much standing timber been destroyed.

Grazing History

The four ungulates of importance in the lower valleys of Banff and Jasper are the Bighorn Sheep (*Ovis canadensis canadensis* Shaw), the Mule Deer (*Odocoileus hemionus hemionus* (Rafinesque)), the Moose (*Alces alces andersoni* Peterson), and the Elk (*Cervus canadensis nelsoni* v. Bailey).

The major part of the diet of mule deer and moose consists of leaves and shoots from shrubs and young trees. In contrast the bighorn sheep are grazing animals, feeding on grasses and forbs. Elk are intermediate and are able to thrive on diets of grasses, shrubs or herbs. Before 1880, elk were abundant in the foothills of the Rockies. Except for one small herd in Jasper, they disappeared from the Alberta Rockies during the 1880's, probably due to severe winters (Flook, 1964).

At the time of park establishment, mule deer, moose and bighorn sheep were more numerous than elk. Elk from Yellowstone Park were released in Banff and Jasper between 1918 and 1920; animals also emigrated over the divide from British Columbia.

The widespread and largely unchecked fires that

occurred previous to the initiation of a fire control policy increased the area of grassland and shrub vegetation and hence the grazing and browsing ranges of these ungulates. These new ranges permitted a steady increase in the populations of all four species. By the 1940's, range conditions became critical especially in the low elevation light snowfall areas where the Douglas fir forests were situated; bighorn sheep, mule deer and elk used these areas as winter grazing grounds. Populations of aspen, a preferred browse species, were severely damaged (Flook, 1964).

Elk reached a population peak in the early 1940's, when range depletion was recognized and herd reductions were begun. Since then, the number of elk has been held in check by annual harvests of up to 700 at Jasper and 400 at Banff in the 1940's, and smaller numbers since. However, stands of aspen do not seem to have recovered; areas killed by bark stripping have little apparent regeneration (Flook, 1964).

Due to the policy of fire protection there will continue to be a gradual decline in suitable browsing and grazing habitat areas as succession to closed canopy forest occurs.

Bighorn sheep graze predominantly on graminoid species during the winter and are therefore usually found on south-facing slopes where the snow depth is minimal. They are known to frequent open Douglas fir stands (Flook, 1964). In summer their diet enlarges to browse and forbs,

especially *Hedysarum mackenzii*, *Astragalus* spp., and *Oxytropis* spp.

The mule deer, unlike sheep, are predominantly browsing animals; their preferred forage species include *Amelanchier alnifolia*, *Populus tremuloides*, *Salix* spp., *Cornus stolonifera* and *Prunus melanocarpa* (A. Nels.) Rydb. (Shepherd, 1960). Many deer remain in the valley bottoms throughout the year, frequenting the shrubby areas and forest edges. Like sheep, they avoid deep snow in winter, and in some areas where the preferred browse has been depleted by elk, they have turned to species of low palatability such as *Arctostaphylos uva-ursi*, *Shepherdia canadensis*, *Juniperus horizontalis* and *Pseudotsuga menziesii* (Cowan, 1947).

Klebenow (1965) studied mule deer in western Montana and found that preferred browse species in that region were *Amelanchier alnifolia*, *Mahonia repens*, *Prunus virginiana* L. and *Ceanothus velutinus* Dougl. Shrubs of intermediate preference were *Arctostaphylos uva-ursi*, *Rosa woodsii*, *Vaccinium membranaceum* Dougl. and *Acer glabrum*. *Physocarpus malvaceus* (Greene) Kuntze, *Prunus emarginata* Walp., *Spiraea lucida* and *Symphoricarpos albus* were not preferred as browse. Klebenow found that as the density of shrubs increases, utilization by mule deer decreases because they prefer to browse in less dense areas. Cowan (1945) stated that young growth of Douglas fir and other conifer species in logged areas in the

coastal forest region of British Columbia, were browsed by the Columbian Black-Tailed Deer (*Odocoileus hemionus columbianus* Richardson) to such an extent that deciduous forest eventually regenerates. He labelled Douglas fir as a species of medium-high importance in the diet of this deer, which is closely related to the mule deer.

The moose also browses throughout the year, with feeding preferences much the same as those listed for mule deer. However, a large part of its summer diet consists of aquatic plants (Flook, 1964). Moose can tolerate greater snow depth than the mule deer or the bighorn sheep. They are most frequently associated with moist, shrubby meadows the year round, and with streams and shallow lakes in summer. They are also found in aspen forests rich in their preferred browse species.

Elk are found in a wide variety of habitats, and their feeding habits are adaptable to a marked degree. At present their diet is composed predominantly of graminoid species in Banff and Jasper; browse species are of secondary importance in summer and of very minor importance in winter. Aspen and other preferred browse species were depleted by the large populations of elk in the 1930's and 1940's, so that the browse used now consists of species of lower palatability such as *Shepherdia canadensis* and *Arctostaphylos uva-ursi* (Flook, 1964).

Flook stated in 1964 that elk and bighorn sheep populations were large in the parks, those of moose smaller

and those of mule deer much smaller in size.

IV METHODS

Preliminary Survey

Aerial photographs (1:40,000), taken in 1949-51, were studied of the areas known to contain Douglas fir, and a list made of the locations of all possible sites. It was found possible to detect stands by comparing their appearance on the photographs with the appearance of other known stands of Douglas fir. Mature Douglas fir forest was found to have a very characteristic appearance, and could usually be distinguished from lodgepole pine or white spruce forest with a little practice. Mature Douglas fir forest usually has a distinctive coarse, 'stippled' appearance on aerial photographs, each stipple being a large fir. The shadows of individual large trees were also very distinctive; Douglas fir having a rounded crown whereas white spruce (the species with which it was usually confused on aerial photographs) had a strongly pointed crown. As a general rule, the older, more mature the forest and the more open the canopy, the easier it was to distinguish the tree species. It is inevitable therefore, that there has been a sampling bias towards more mature stands; young immature stands could only be detected by personal inspection. A list of aerial photographs on which stands are located may be found in Appendix

2, page 267.

A survey of potential sites, made in May 1966, confirmed or rejected them as the locations of stands suitable for further study. This preliminary survey indicated that mature Douglas fir populations in the lower valleys of the two parks were exceeded by those of white spruce, lodgepole pine and aspen. All three of these species form extensive, pure and mixed stands throughout the region, and forests in which Douglas fir was the most prominent tree were not common. Douglas fir was usually confined to south-facing slopes, and the tops of dry ridges in the lower valleys of the parks. Its potential habitat in the area is strictly limited, and acceptable sampling sites were not abundant.

It was decided that only about 20 stands could be sampled in the three-month period available. These 20 stands were progressively selected and sampled during the summer of 1965 from the list of potential stands compiled during the preliminary survey (Figs. 2 and 3).

This selection was made in the field, by accepting or rejecting each stand in turn by reference to a list of selection criteria. These criteria were intended to insure that every stand was representative of the Douglas fir forest of the area. Towards the end of the summer it became apparent that the 20 stands sampled would include most of the potential sites. The criteria for selection of stands were as follows:

(1) Presence of Douglas fir throughout an area equivalent to at least 500 x 500 feet and representing at least 50% of the total tree volume, based on subjective observation.

(2) No evidence of major human disturbance. Inasmuch as the research was to be carried out within National Parks, it was considered possible and desirable to avoid stands that were too close to cleared areas, camping or construction sites, etc., or crossed by well-travelled trails or footpaths. It was suspected that large areas of original Douglas fir forest had already been cleared or altered in various ways (eg. conversion to campgrounds, dissection by roads, riding trails, power lines etc.).

(3) Areas recently disturbed by epidemics of diseases, fires or lumbering were avoided. This last criterion shouldn't have applied much in a National Park, but two sites were found where several trees had been cut; how recently was difficult to ascertain.

(4) The stands were required to have a reasonable uniformity of topography, aspect and slope angle, ensuring no major environmental discontinuities. It was found impossible to avoid occasional wide ranges of slope angle

in limited sections of some stands; indeed Douglas fir ecosystems appear to be common in "irregular" habitats.

Sampling Scheme

Stands have been numbered from 1 to 21 in chronological sequence according to the sampling dates. The initials 'B', 'J' and 'W' have been inserted after each stand number in the text to indicate park locations (B = Banff, J = Jasper and W = Waterton).

Notes were made on the geographical location of the stand, including landmarks as well as latitude and longitude. The approximate limits of the area suitable for stand sampling were ascertained and then a long axis was chosen to correspond with the maximum possible length of the stand. This long axis was marked out into 100-foot lengths with a 300-foot band chain, and its compass bearing recorded to ensure straightness, and help in laying down other lines at right angles to the axis. After completion of the stand, two permanent marker stakes of hollow metal piping were hammered into the ground, one at each end of the portion of the long axis incorporated into the stand, to facilitate study on future dates.

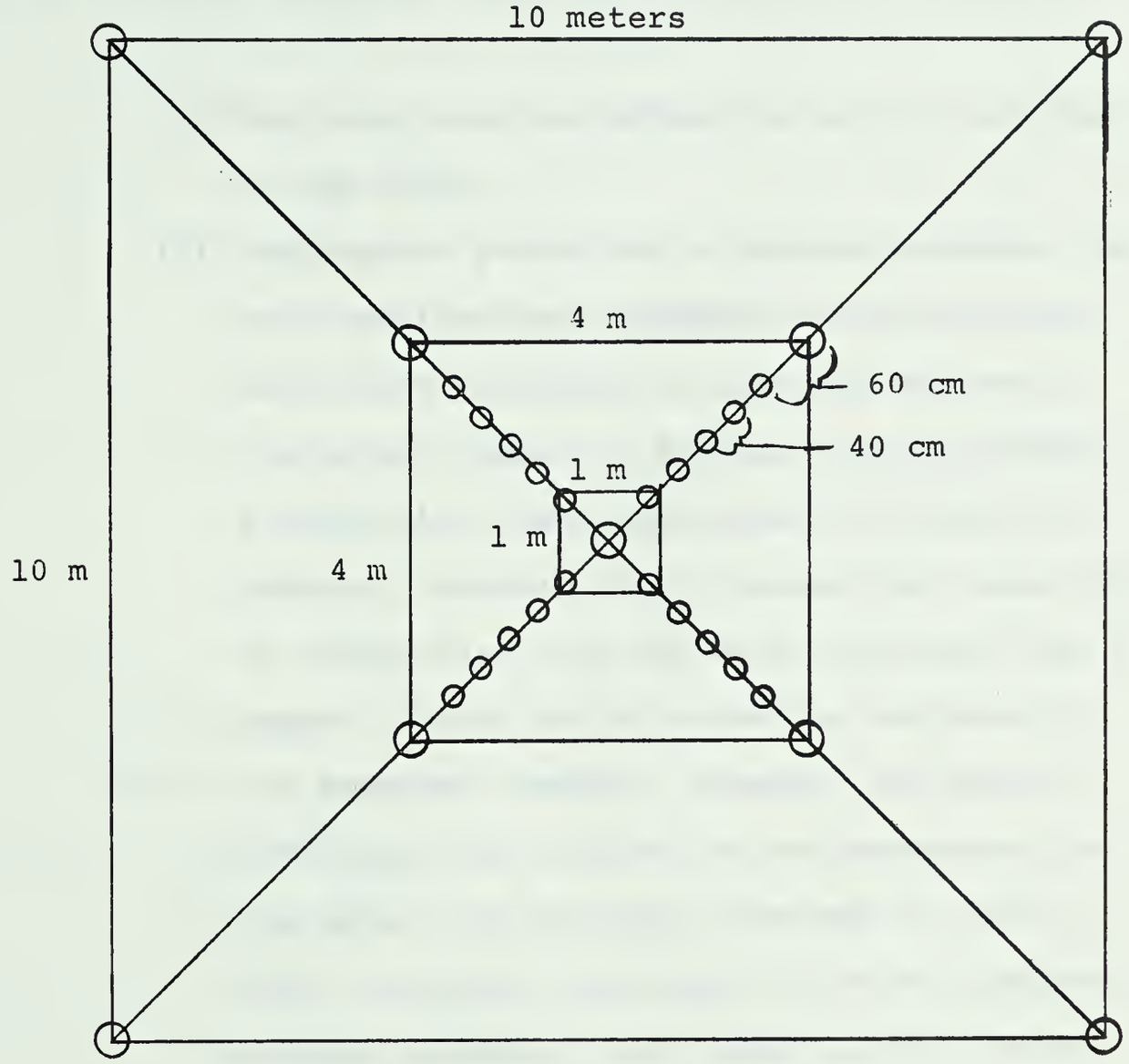
The long axis was used as a base line for dividing the total possible stand area up into sections of equal area, in each of which a fixed number of random points could

be located, and used as centers of sampling quadrats. The position of each random point was determined using two coordinate numbers read from a random numbers table. The first number gave the distance along that section of the long axis; the second gave the lateral distance of that point from the axis. The asymmetrical shape of some stands made it necessary to modify this procedure on occasions, but the principle of proportionate sampling of areas was adhered to at all times.

All stands were sampled to a density of one random point per 8000 square feet. On most occasions, it was found convenient to sample areas of 200 x 200 feet, or the equivalent, and select five random points from this area. This restricted random sampling method had the advantage over unrestricted random sampling in that it was possible to extend the sampling progressively over the suitable site until the required level of sampling accuracy had been reached, and terminate with the same sampling intensity in all stands (one random point per 8000 square feet). After the required sampling efficiency was reached, the length of the original long axis not incorporated into the area sampled was considered to be outside the stand area, and so disregarded. In this way, the area of the stand actually sampled was usually smaller than the area potentially available.

At each random point, three nested quadrats were set up to sample the floristic composition and structure of the vegetation strata (Fig. 5).

FIGURE 5. SIZE AND PLACEMENT OF NESTED QUADRATS



NOTES: ○ cover points (9) for tree stratum

○ cover points (20) for all other strata

Square quadrats were used in preference to rectangular or circular sampling areas for the following reasons:

(1) They were more convenient to lay out and use in the field.

(2) Rectangular plots have a greater perimeter per unit sampling area; therefore more time and care would be needed in sampling because of the larger number of decisions as to whether a particular plant was inside or outside the quadrat. Bormann (1953) showed that some form of rectangular plot was more efficient than a square quadrat due to a smaller variance in the sampling results. However, the extra efficiency was thought not to compensate for the extra time and care involved in using them. Circular areas would have an absolute minimum perimeter, but three nested circles would be extremely difficult to use in practice, and also difficult to delimit satisfactorily in tall shrubs and herbs.

(3) Other workers in this part of the Rocky Mountains had already used or intended to use square quadrats, and therefore some standardization of procedure was desirable to allow for future comparison of results.

Quadrat sizes were as follows:

(1) 10 x 10 meter quadrats for the tree (stems more than 3 inches DBH) and tall shrub strata, to include all shrubs over five feet high.
(2) 4 x 4 meter quadrats for the medium-sized shrubs (all woody vegetation between 6 inches and 5 feet high).
(3) 1 x 1 meter quadrats for dwarf shrubs (decumbent habit and less than 6 inches tall), herbs and vascular cryptogams.

The size of the quadrats used had to be adequate to avoid excessive exclusion effects between species in the same stratum, and also small enough to be convenient to use.

The most efficient method of laying out the nested quadrats was to use previously marked and measured diagonals.

These diagonals consisted of nylon rope, marked off at regular intervals to indicate the position of quadrat corners. The corners of the 10 x 10 and 4 x 4 meter quadrats were marked by pins and decisions on edge-effects made by sighting between corner pins. The sides of the 1 x 1 meter quadrat were delineated with wooden laths. The nylon ropes were checked periodically for stretch etc., and were found to be reliable under quite stringent field usage.

It was considered that the most important stand parameter amenable to rapid calculation was tree density.

Therefore, the stand area was sampled sequentially until a previously fixed minimum standard error of the mean tree density per quadrat was obtained.

The fixed standard error was set at 10% of the mean density of all trees, and 15% of the mean density of Douglas fir. It was expected that total tree density would vary somewhat less than that of any single tree species, due to the apparently aggregated condition of many of the stands. A reasonable estimate of how many quadrats would be required to obtain a representative sample was determined after the first fifteen quadrats were tallied as follows. The mean and standard deviations for the samples were calculated, and the quantity

$$\frac{\text{Standard Deviation}}{\sqrt{N-1}} = \text{Standard Error}$$

used as an estimate of the standard error of the mean of an infinite population (N = number of observations) (Schumacher and Chapman, 1948, p. 195).

The standard error had been set at 10% (or 15% for Douglas fir alone) of the mean; thus 'N', the only unknown, was calculated by solution of the equation. Quadrat observations were then terminated when the required sampling accuracy was reached. The sampling accuracy was then confirmed by calculating the standard error of the results obtained.

Many of the potential sampling areas were very limited in extent, and the tree populations therefore of finite size. Consequently the standard error actually obtained from the quadrats sampled was considerably less than the set figure of 10% or 15%. This would result in an even higher sampling accuracy than originally intended (Schumacher and Chapman, 1948, p. 52).

Observations at Sample Points

Vegetation Analysis

1. Frequency

A list of plant species present in the appropriate -sized quadrat was compiled. To avoid oversampling species with a decumbent growth habit, plants had to be rooted inside the limits of the quadrat to be counted. In cases where identification was impossible or doubtful in the field (eg. many bryophytes and lichens), specimens were collected for later identification. The Frequency list was used for calculating the quadrat Frequency of species in the stand. The Frequency values are a measure of the distribution patterns of species populations in the stand.

2. Density

It was also necessary to have some measure of the population size of each species in a stand, to complement Frequency. However, it was not practically feasible to make

density counts for species other than trees and shrubs, because of the difficulties involved in defining and recognizing individuals, or in deciding on arbitrary density units for many species of herbs, especially grasses and sedges.

Tree counts were tallied by species, in living and dead categories, in the 10 x 10 meter quadrat. Similar counts were made of tree saplings (1-3 inches DBH). Density counts were made on shrubs in the 4 x 4 meter quadrat, by recording both number of individuals and number of stems for most species, but stem number only for species like *Rosa acicularis* and *Spiraea lucida*, which do not often develop into multistemmed individuals. In this quadrat, density counts were made of tree transgressives (less than 1 inch DBH, and 6 inches to 5 feet in height). On rare occasions certain shrubs, notably *Shepherdia canadensis* and *Salix* spp., topped the 5 foot mark, and were counted in the 10 x 10 meter quadrat. Density values could then be calculated by species, as stems per 100 square meters for trees, saplings and tall shrubs, and as individuals and/or stems per 16 square meters for shrubs and transgressives. In the 1 x 1 meter quadrat, no counts were made of individual herb plants or clones for the reasons already stated.

The diameters of living trees in the 10 x 10 meter quadrat were measured at a height of 4 feet above the ground (DBH value), using a Lufkin tree tape. Similarly the DBH values of all saplings were taken with 12 inch Swedish tree

calipers. These diameters were later divided into 3-inch size-classes, and the numbers of trees of each species falling into each class enumerated. A DBH size-class distribution for each stand could then be plotted in Frequency polygon form to complement the absolute density values of each species.

Density and Frequency gave a good estimation of the numerical and distributional attributes of the species populations inhabiting the stand. To obtain a more satisfactory assessment of standing crop and photosynthetic area of these populations, sampling estimates were made of the amount of ground covered by each species.

3. Cover

Cover estimates for strata other than the tree canopy were obtained by the point quadrat method using 20 points per quadrat (Greig-Smith, 1964, p. 6). The points were marked on the nylon rope diagonals at fixed intervals, five on each arm between the center point and the corner of the 4 x 4 meter quadrat (Fig. 5). A No. 14 knitting needle was lowered adjacent to the mark and the species touched by the needle recorded. This method proved very satisfactory for herbs, dwarf shrubs and vascular cryptogams, but became increasingly less so for taller plants. Consequently, medium and tall shrub cover was recorded not by the specie's touching the needle but by visual sighting over the needle

inserted in the ground at that point.

The most important error inherent in this method derives from the finite diameter of the needle itself, resulting in an overestimation of the cover value, especially for fine-leaved species. A true cover value could only be obtained by using a needle of infinitely small diameter (Goodall, 1952), or a sighting device. This error was thought to be relatively unimportant as the same sized needle was used throughout the study and observations were used for comparison purposes within this thesis only. Other more subjective errors invariably associated with this type of cover estimation would outweight this objection. The cover of each species in the stand was calculated as a percentage of the total possible "hits" (cover sampling points).

Cover of the tree canopy was estimated by two methods. A purely visual method was used by recording presence or absence of foliage directly above each of nine fixed points in the quadrat area (Fig. 5). These nine points were the center and the corners of the 4 x 4 meter and 10 x 10 meter quadrats. The percentage total tree cover as well as the cover of individual species was then calculated as for herbs and shrubs.

4. Canopy cover from vertical photographs

The point quadrat method was thought to be too subjective, especially for the thin cover provided by aspen

and lodgepole pine. Therefore another method was tried, based on a vertical photograph of the tree canopy taken from the center point. Using a spirit level to ensure that the camera orientation was vertical, one photograph was taken at each quadrat, using an Ansco 'Readyflash' camera with a lens angle of about 38 degrees. Size 620 black and white film was used for all photographs.

This method is an adaptation of that used by Brown and Worley (1965), and the method of sampling the photographic print modified from Lemmon (1956).

After development, the 5.6 x 8.4 cm photographic prints were sampled using a grid of 10 equidistant points inside a circle of radius 14 mm (Fig. 6), and a percentage total tree cover calculated for the stand. Individual tree species were often impossible to differentiate on these prints. Figure 7 demonstrates the effect of using sampling circles of differing radii. It was generally found that the larger the sampling circle and the higher the stratum, the greater was the peripheral distortion due to the field of view including more and more lateral vegetation. Consequently the larger the sampling circle, the greater is the tendency towards overestimation. Further discussion of this method can be found in Appendix 7.

5. Basal area

To obtain a measure of the proportion of ground surface occupied by the trunks of the tree species, basal

FIGURE 6. POINT SAMPLING OF VERTICAL PHOTOGRAPHS BY NESTED CIRLES

Circles of radii 14, 19.8, 24.2 and 28 mm have 10, 20, 30 and 40 sampling points respectively.

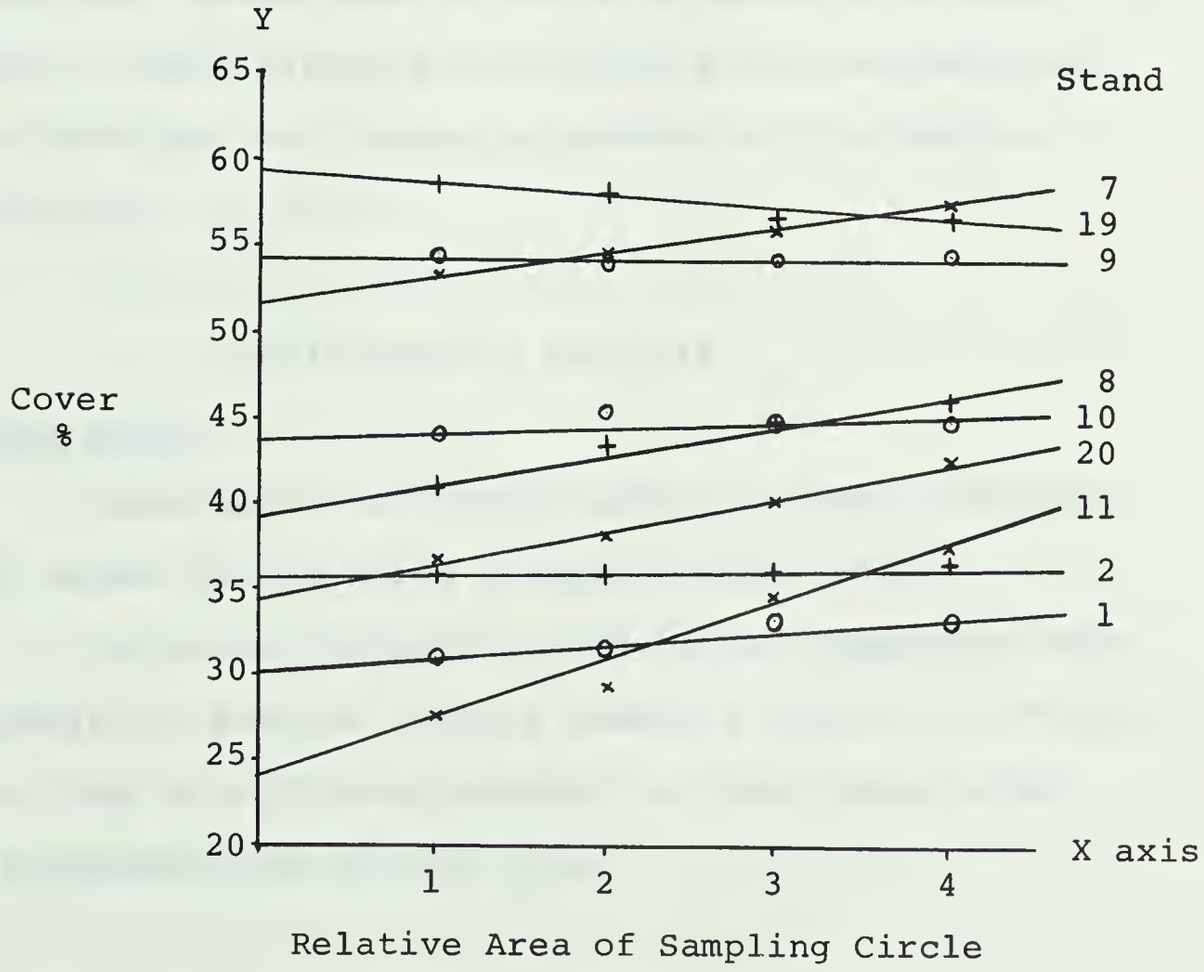


FIGURE 7. TOTAL TREE COVER ESTIMATES OF STANDS AT BANFF USING THE VERTICAL PHOTOGRAPH METHOD

area measurements were made from the center point using a 10X Bitterlich prism (Grosenbaugh, 1952).

The basal area of each tree species (in square feet per acre) gave a useful estimate of the absolute standing crop and the relative importance of that species in the stand.

6. Dispersion of trees

The distance from the quadrat center point to the center of the nearest Douglas fir tree was measured to the nearest inch. The DBH and height of that tree were measured and recorded. Height was estimated by means of a Haga altimeter. These distance measurements were subsequently used to describe the dispersion pattern of the Douglas fir population (p. 107).

Environmental Analysis

1. Slope angle

Measurements of slope angle were made from the quadrat center points using a Leupold Abney level.

On several occasions, undulating topography made it necessary to average several readings taken in different parts of the 10 x 10 meter quadrat to give a mean slope angle representative of that site.

2. Aspect

Using a Silva Ranger pocket compass, a measurement

was taken of the aspect of (direction faced by) the average slope inside the 10 x 10 meter quadrat.

3. Soil temperature

The soil temperature was recorded near the center point, and at a depth of four inches, using an 8 inch probe thermometer.

4. Air temperature

The air temperature was recorded at a height of about four feet, using an alcohol-in-glass thermometer. Care was taken to ensure that direct sunlight did not strike the thermometer bulb, and the time of temperature measurement was noted.

General Observations Made in the Stand

1. Presence list

A list of all vascular plant species in the stand area was compiled, inclusive of all species observed to be present, as well as those previously located in the random point quadrats.

For bryophytes and lichens, only those species making a notable contribution to the ground cover (or rocks and logs on the ground surface) were noted; as a consequence many small turf mosses and *Cladonia* species among others have been missed.

Certain species collected in the field were not adequate for identification beyond genus, so the following were listed as such: *Cladonia* spp., *Usnea* spp., *Salix* spp., *Taraxacum* spp. Confusion in the identification of *Poa* spp., due to many suspected hybrids between *Poa interior*, *Poa palustris* and *Poa pratensis* resulted in specimens of the genus being listed as *Poa* spp. In actuality, most of the specimens collected appeared to be *Poa interior*.

Identifications of angiosperms, gymnosperms and ferns were made initially using Moss' "Flora of Alberta" (1959) and later confirmed or corrected by Mr. J.G. Packer, Department of Botany, University of Alberta, Edmonton. Tentative identifications of some of the more common bryophytes and lichens were confirmed or corrected by Dr. C.D. Bird, Department of Biology, University of Calgary, Alberta, who also identified the bulk of the collection.

Nomenclature follows that of E.H. Moss, "Flora of Alberta" (1959); C.D. Bird, "A Preliminary Flora of the Alberta Sphagna and Musci" (1964); R.M. Schuster, "Boreal Hepaticae; A Manual of the Liverworts of Minnesota and Adjacent Regions" (1953); C.D. Bird, "A Catalogue of Lichens Reported from Alberta" (1966).

2. Qualitative and semi-quantitative observations

A number of qualitative or semi-quantitative observations were made in the stand pertaining to community structure and the population size of the various plant

species.

Notes were made on the mean maximum height of the major shrubs, together with observations on the amount of grazing, trampling of vegetation and any other evidence of animal activity. The latter observations were of necessity brief and incomplete, as the study was primarily concerned with the primary producer level of the ecosystem, and not the effects of higher trophic levels on producers.

Each shrub and herb species was evaluated on four phytosociological scales relating to (A) Cover-Abundance, (B) Vitality, (C) Sociability, (D) Periodicity.

The Cover-Abundance scale was a modification of that found on page 34 in Fuller and Conard's translation of J. Braun-Blanquet, "Plant Sociology" (1932) as follows:

(A) Cover-Abundance scale

R - Rare

\+ - Common, but cover less than 1%

1 - Abundant, with cover between 1 and 5%

2 - Abundant, with cover between 5 and 15%

3 - Abundant, with cover between 15 and 25%

4 - Abundant, with cover between 25 and 50%

5 - Abundant, with cover between 50 and 75%

6 - Abundant, with cover between 75 and 100%.

The other three scales were used, unmodified, as in the above publication (pages 46, 36 and 47).

(B) Vitality

1) Well developed in stand, regularly completing life cycle
2) Abundant and well established but usually not completing life cycle
3) Scattered, and spreading only feebly or not at all; rarely completing life cycle
4) An unsuccessful adventive; occasionally germinating, but not flowering or increasing vegetatively.

(C) Sociability

1) Growing as single distinct individuals
2) Growing in small groups or tufts
3) Growing in patches or small cushions
4) Growing in intensive patches or forming extensive carpets
5) Growing in extensive masses, and as pure stands of wide extent.

(D) Periodicity

Fol. - In foliage only

Fl. - Flowering

Fr. - Fruiting

B. - Flower buds developed, but not yet opened

SF. - Leafless.

Slash marks were used where more than one symbol was required. It was hoped that these scale values, based entirely on visual interpretation, would help in clarification of the structure and phytosociology of the stands. Tree species, bryophytes and lichens were assessed for Cover-Abundance only.

3. Stand history and tree ages

Increment cores were taken from at least twelve trees per stand, using a 20-inch DJOS increment borer. The trees were selected to represent the major size-classes present by species. At least six of these and more usually eight or ten of the cores were from Douglas fir, as the number of cores taken per species were made roughly proportional to that species' relative stand volume. Included in the total was a core from the largest tree of each species. The DBH and height of each tree were also recorded.

Examination of the cores gave an estimation of the age of the stand, as well as indications of any major climatic fluctuations, fires, etc.

4. Light readings

As close to noon as possible, light readings were taken at about 50-foot intervals along the long axis of the

stand. A Weston Master IV exposure meter was orientated to point vertically, and held at arms length at each selected spot, the observer facing south. Although these spots were selected systematically, they were chosen irrespective of the local topography, canopy, slope, etc., so that they could be considered representative of the stand as a whole.

The mean was calculated from the 16 to 20 values obtained for the stand, and expressed as a percentage of the light reading taken at the same time in an open location in that area.

This method was subject to considerable error, in that wide variation was to be expected in readings, partly due to factors other than canopy cover. For example, wind movement shifts the position of the canopy and results in sun flecks, and a very slight deviation from the horizontal by the plane of the exposure meter resulted in sudden, sharp changes in the reading. A prohibitive number of readings would have been necessary to make this method accurate enough to use for anything except rough comparative purposes (Oosting, 1956, p. 87).

As an estimate of canopy cover, it is probably less accurate than the values obtained by the point quadrat and vertical photograph methods already described.

5. Elevation

Readings on the elevation of each stand were

obtained using a Taylor altitude barometer. The readings were taken at the lower and upper limits as well as the approximate center of each stand.

6. Soil

A soil pit was dug at as representative a site as possible, to a depth of at least 18 inches, and a soil sample taken of each distinct horizon in the profile. A few drops of toluene were added to each soil sample to kill or inhibit the activities of bacteria and other microorganisms. The depth and thickness of each horizon was recorded, together with general notes on colour, appearance, texture, water content, etc.

Usually five samples were taken from each pit, one each of litter and humus, and three mineral soil samples. They were subsequently air-dried, sorted into fractions, weighed and later analyzed in the laboratory as follows.

The sample was sieved through successive sieve meshes of size 3/4 inch, 1/4 inch and 2 mm, and the percentage of the sample weight in each size class was calculated.

The larger rocks in the "more than 3/4 inch" diameter class were identified as to rock type by Dr. J. Westgate, Department of Geology, University of Alberta, Edmonton.

A number of analyses were carried out on the less than 2 mm fraction:

(A) A portion of the sample was air-dried at

about 100°C to constant weight. Each succeeding analysis of the sample could then be converted to an oven-dry basis.

(B) Soil Texture:

The percentage weight of soil in each of the following particle size-classes was determined by mechanical analysis (United States Department of Agriculture classification).

Sand	2.00 - 0.05 mm diameter
Silt	0.05 - 0.002 mm diameter
Clay	less than 0.002 mm diameter.

The hydrometer method used was essentially that of G.J. Bouyoucos (1951), with some of the modifications proposed by C.T. Youngberg (1957):

a) 10 mls of 5% Sodium Hexametaphosphate solution was used as a dispersal agent instead of 5 mls of 1 N solution.

b) The soil suspension was slaked with the dispersal agent for a minimum of 12 hours, and not 2 hours.

c) The suspension was agitated in a reciprocal shaker for one hour at the commencement of shaking and for a further one-half hour immediately prior to transfer to the soil cylinder.

(C) Field Capacity:

The percentage moisture of each sample at field capacity was determined with a porous plate apparatus, at a pressure of one-third of an atmosphere.

(D) Permanent Wilting Percentage:

The percentage moisture of each sample at permanent wilting percentage was determined with a pressure membrane apparatus, at a pressure of 15 atmospheres.

For both of the above determinations, the methods used were those described in the United States Department of Agriculture handbook No. 60 (1954), and were conducted in the Soil Science Department, University of Alberta, with the assistance of Dr. J.A. Toogood and Mr. G. Beke.

(E) Available Water:

The difference between the field capacity and the permanent wilting percentage of each soil sample was used as a measure of the potential water availability.

(F) Chemical Analysis:

A chemical analysis of the soil samples was made by the Agricultural Soil and Feed Testing Laboratory, University of Alberta.

This analysis included the following determinations:

a) Available nitrogen (in lbs per acre)

b) Available phosphorus (in lbs per acre)

c) Available potassium (in lbs per acre)

d) pH value

e) Soil conductivity (in mmhos)

f) A semi-quantitative estimation of free lime

g) a semi-quantitative test for sulphate.

The methods used were those recommended in the Methods of Analysis Handbook of the American Association of Agricultural Chemists or modifications of them; further details may be obtained from the Director of the Agricultural Soil and Feed Testing Laboratory, University of Alberta, Edmonton.

V DESCRIPTION OF VEGETATION

A total of 140 vascular species was identified in Banff and Jasper stands, including 6 trees, 13 shrubs and 121 herbs and dwarf shrubs. An additional 20 species were present in Stand 21W at Waterton (1 tree, 4 shrubs and 15 herbs).

The Presence class distribution of the 140 species at Banff and Jasper shows that 70 species were present in 20% or less of the 20 stands studied (4 stands or fewer), whereas only 15 species had a Presence of 80% or more (Fig. 9). This indicated that relatively few vascular plant species are constantly present in the Douglas fir ecosystem defined by the selection criteria.

Two of the six trees, 6 of the 13 shrubs but only 8 of the 121 herbs and dwarf shrubs were represented in the 80 - 100% Presence class, illustrating the floristic uniformity of the tree and shrub strata in contrast to the floristic heterogeneity of the herb and dwarf shrub stratum.

The histogram of Frequency classes for the 105 vascular species represented in quadrat data shows that the large majority of species have a very scattered and limited distribution (Fig. 8). Ninety-three species have mean Frequencies for the 20 stands of 20% or less. Only Douglas

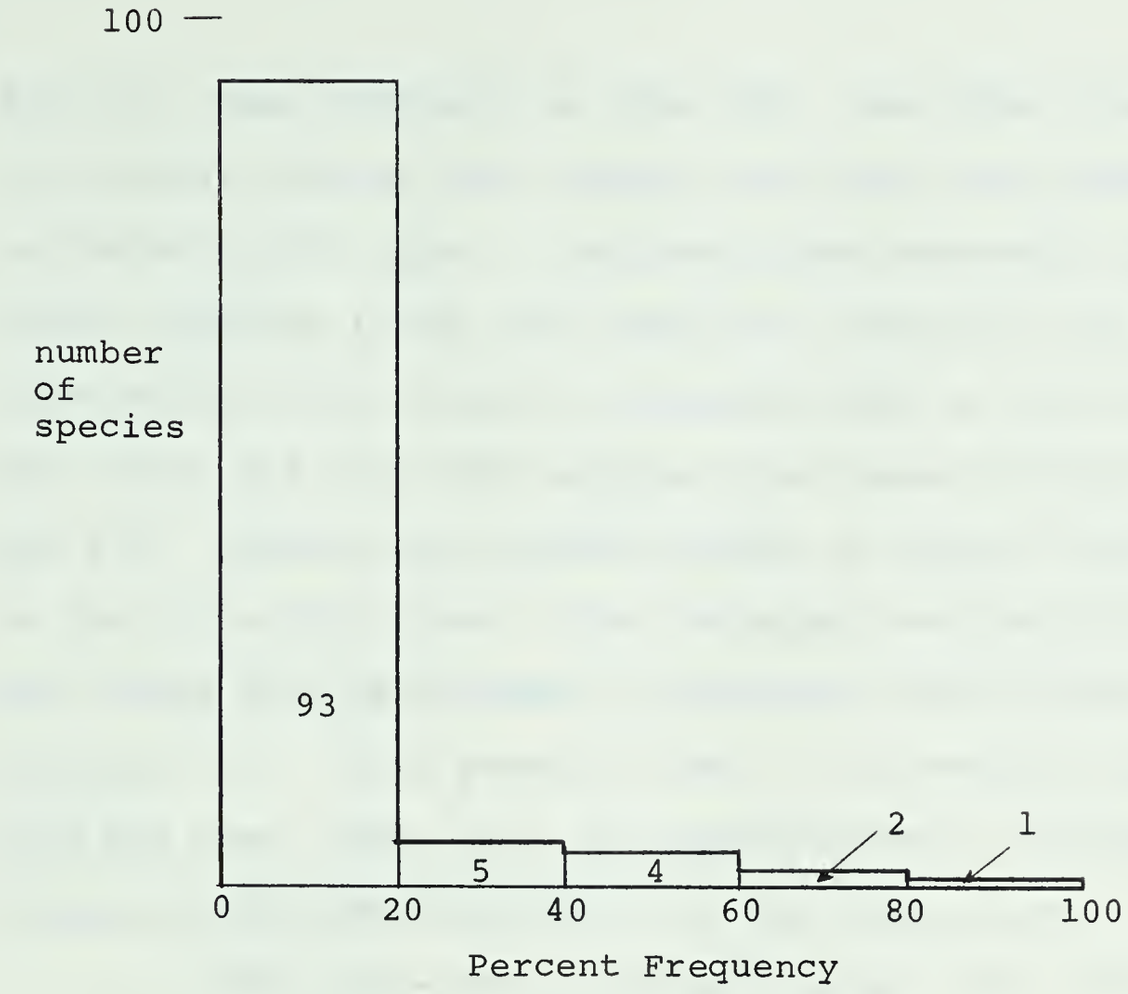


FIGURE 8. QUADRAT FREQUENCY OF VASCULAR SPECIES

Excluding Stand 21 (Waterton)

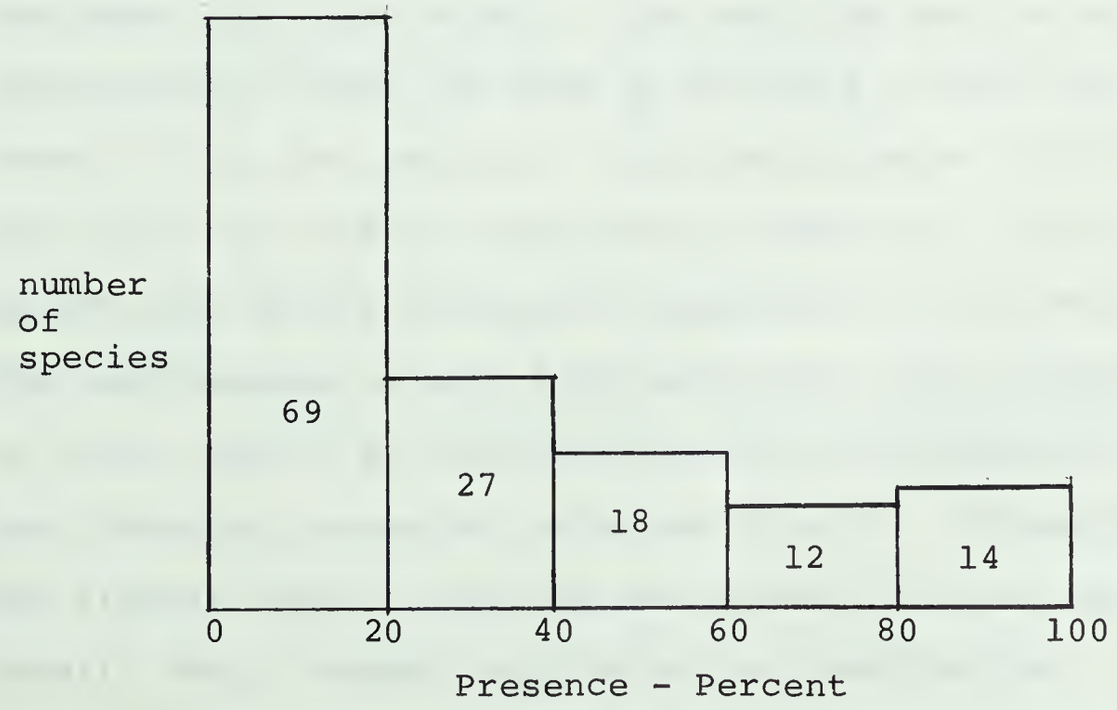


FIGURE 9. PRESENCE HISTOGRAMS OF VASCULAR SPECIES

Exluding Stand 21 (Waterton)

fir has a mean Frequency of over 80%. One shrub (*Rosa aciculariss*) and one herb (*Elymus innovatus*) are present in the 60 to 80% class. One tree (*Pinus contorta*), two shrubs (*Spiraea lucida* and *Shepherdia canadensis*) and one dwarf shrub (*Arctostaphylos uva-ursi*) make up the 40 to 60% class, and five herb species have values between 20 and 40%. Because the smallest number of species occurs in the 80 to 100% class, this histogram does not follow the normal form as proposed by Raunkaier (Greig-Smith, 1964, p. 16). It is possible that if the sampling quadrats had been larger then the distribution of Frequency classes would have been closer to the normal form.

The cover-stratification diagram (Cain and Castro, 1959, pp. 223-5) shows the total average cover and height of each stratum (Fig. 10). This diagram clearly shows that the tree stratum forms the major photosynthetic surface and dominates the lower strata. The two tree species with mean Frequencies of over 20% make up the bulk of the 45.4% mean cover of the tree stratum. The shrub stratum, with a mean cover of only 5.9%, is relatively unimportant, low in height, and mainly confined to openings in the tree canopy. The herb stratum is much more extensive, with a mean cover of 30.2%, but it is very heterogeneous in composition as the Frequency histogram indicates (Fig. 8). Bryophytes and lichens, with a combined mean cover of 14.4%, are usually few in number and limited in distribution.

The combined cover of all the subordinate strata

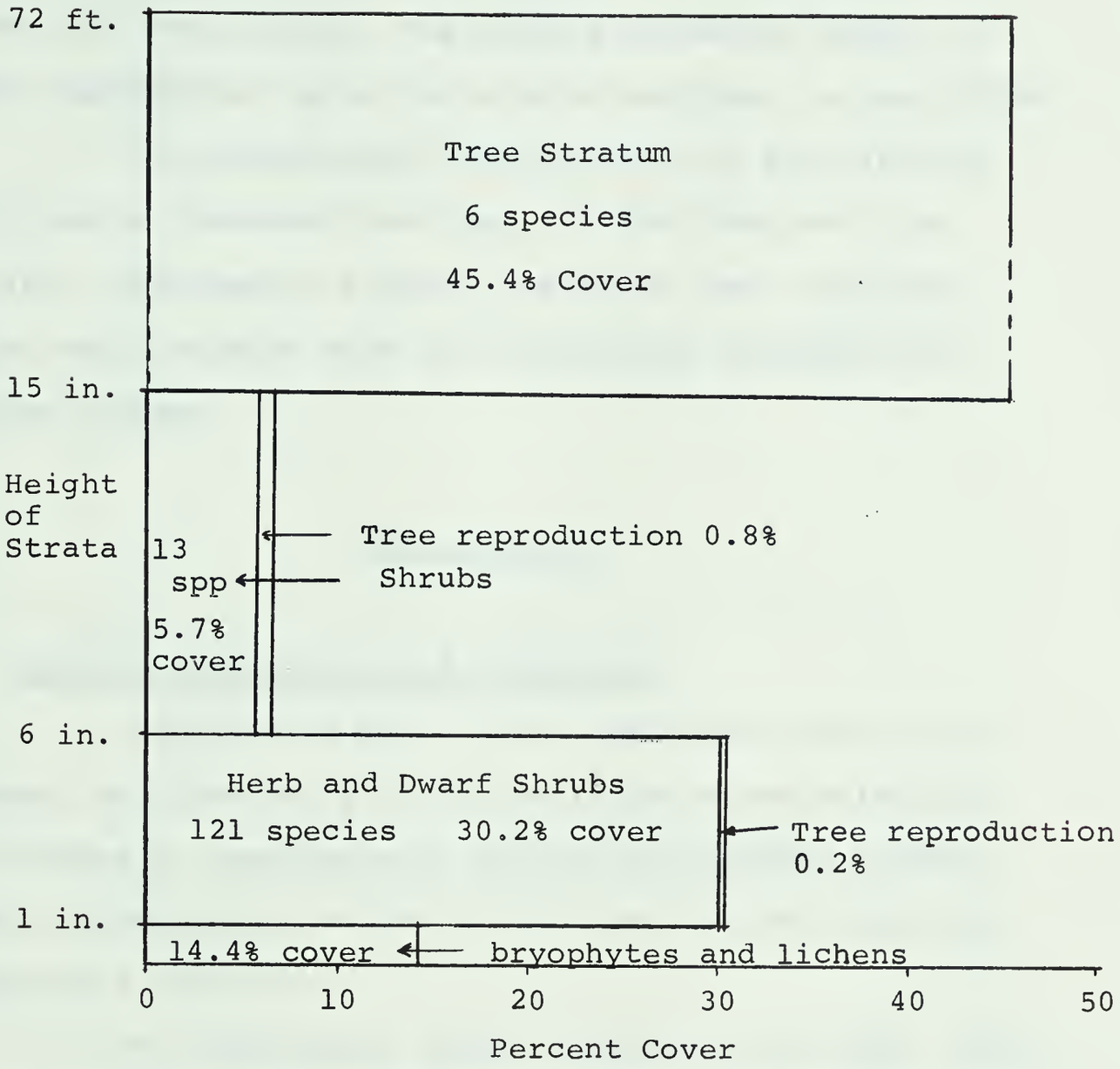


FIGURE 10. COVER-STRATIFICATION DIAGRAM OF DOUGLAS FIR FOREST IN BANFF AND JASPER NATIONAL PARKS

is only 50.5% so that, allowing for some overlap, at least 50% of the ground surface is barren of living vegetation under the tree canopy. The cover provided by stages in tree reproduction up to the size of saplings is negligible.

The composition and structure of each stratum will now be discussed starting with the dominant tree stratum, progressing through the shrub, herb and dwarf shrub and finishing with the terrestrial bryophyte and lichen stratum.

Tree Stratum

1. Species composition and importance

Douglas fir was the most prominent tree in all stands, as dictated by the criteria for stand selection. The degree of prominence of Douglas fir becomes evident when the importance values of species in each stand are considered (Table 4).

The importance value (Curtis and McIntosh, 1950) was formed by the summation of the relative values (as percentages) of density, quadrat Frequency and basal area to give a maximum possible value of 300. It is more comprehensive as a measure of the relative importance of a species in a stand than any of its component parameters taken singly, but suffers from the disadvantage that different types of population and stratum structure may give rise to similar values (Greig-Smith, 1964, p. 142). However,

TABLE 4. IMPORTANCE VALUES[a] OF TREES

Stand	*Pseudotsuga menziesii*	*Pinus contorta*	*Picea glauca*	*Populus tremuloides*	Other Species
1B	246.2	52.7	1.1		
2B	163.3	102.6	23.7	10.4	
3J	214.5	78.3		7.2	
4J	282.7	17.0	0.3		
5J	282.7	17.3			
6J	188.4	32.8	65.2	13.6	
7B	275.9	13.7	4.9	5.5	
8B	185.8	96.4	17.8		
9B	236.6	57.2	6.2		
10B	237.4	42.5	3.7	16.4	
11B	145.9	127.4	26.7		
12J	189.3	6.8	101.0		2.9[b]
13J	220.9	67.1	8.5	3.5	
14J	217.6	50.5	12.4	19.5	
15J	257.5	42.5			
16J	150.5	97.6	41.2	10.7	
17J	261.6	37.2	1.2		
18J	236.9	50.6		12.5	
19B	200.8	95.6	3.6		
20B	224.6	55.7	3.7	16.0	
21W	234.5	54.8		3.6	7.1[c]
Mean	221.6	57.0	15.3	5.6	0.5

NOTES: [a] Importance Value = Relative Basal Area + Relative Density + Relative Frequency as percentages

[b] *Betula papyrifera*

[c] *Abies lasiocarpa*

this disadvantage is even more apparent in using each of these parameters alone.

The importance value (IV) of Douglas fir varied from a minimum of 145.9 in Stand 11B to a maximum of 282.7 in Stands 4J and 5J, the latter being near-pure populations of old fir trees.

Lodgepole pine was present in all 21 stands and was second in rank in 19 of them. Only in Stand 11B did the IV of pine come close to that of the fir (Douglas fir 146, lodgepole pine 127).

White spruce had the second highest IV in Stands 6J and 12J, the only two in which its IV exceeded 50, but in neither did it come within 50 IV units of the Douglas fir. Spruce was absent completely from only four stands.

Aspen was of very minor importance, its maximum IV being only 19.5 in Stand 14J; it was absent completely from eight stands.

2. Height

The maximum height of the tree stratum, based on the tallest tree in the stand, varied from a low of 54 feet in Stand 1B to a high of 142 feet in Stand 5J (Table 5). A second measure was the "average maximum height of a stand", defined as the mean of the tallest 25% of the trees measured. This value varied from 45 feet in Stand 1B to 100 feet in Stand 14J.

In only three stands was a Douglas fir not the

TABLE 5. HEIGHTS OF TREE STRATUM COMPONENTS

Expressed in feet.

	Pseudotsuga menziesii				*Pinus contorta*		*Picea glauca*	*Populus tremuloides*
Stand	Mean[a]	St. Deviation	Mean of Tallest 25%[c]	Maximum[b]	Mean[a]	Maximum[b]	Maximum[b]	Maximum[b]
1B	31.1	8.59	45.0	54	41.5	46	40	
2B	38.0	16.36	59.8	76	47.5	60	40	41
3J	40.0	15.63	65.5	84	45.5	52		36
4J	51.7	15.41	86.7	122	48.3	64		
5J	65.9	13.10	97.0	142	47.7	64		
6J	41.4	17.47	78.9	120	*	63	62	35
7B	50.3	14.03	77.9	95	*	58	50	36
8B	52.6	9.41	61.7	66	49.0	57	51	
9B	35.7	6.92	52.4	67	46.3	49	54	
10B	42.0	11.44	59.2	68	54.0	64	70	48
11B	47.8	12.99	61.6	64	53.5	67	66	
12J	56.3	21.28	88.4	134	*	50	110	
13J	59.8	29.11	93.1	130	55.7	63	53	40
14J	52.7	28.30	100.7	134	43.3	73	93	36
15J	46.4	11.22	58.4	69	43.0	49		
16J	58.1	19.67	84.3	100	50.7	60	68	48
17J	62.3	25.62	99.7	118	53.0	61	62	
18J	53.7	17.94	76.4	81	40.7	68	39	40
19B	49.1	12.39	59.6	65	58.7	70	55	30
20B	30.5	10.36	58.7	84	39.0	56	38	41
21W	46.6	10.44	59.4	76	51.3	55		
Mean	48.2		72.6	93	49.5	59	59	39

NOTES: * only one tree sampled

[a] 'mean' is mean of all trees (over 3 inches DBH) sampled in the stand, by the "nearest individual" method for Douglas fir (ie random), but only for specially selected trees for other species

[b] 'maximum'. As trees were not selected for sampling on height criteria alone, this value will not necessarily be the tallest tree in the stand

[c] 'mean of tallest 25%' of Douglas fir trees sampled was of 5 to 8 trees, and was thought to represent the "mean-maximum" height of the stand.

tallest tree. The tallest white spruce in Stands 10B and 11B and lodgepole pine in Stands 11B and 19B were a few feet taller than the Douglas fir maximum. However these were only isolated trees, and didn't alter the fact that the prevailing height of the tree stratum in all stands was very largely a function of the heights of the more mature Douglas firs.

The standard deviation of the mean height of Douglas fir tree populations indicated that some stands were very uniform throughout. For example, Stands 8B, 9B and 21W had low values of 9.41, 6.92 and 10.44 feet respectively. More of the stands had much larger standard deviations, indicative of a more general irregularity of the tree canopy. There was a slight correlation between mean height and standard deviation, indicating that the tree canopy becomes increasingly irregular with increasing height, and presumably age.

The maximum heights of lodgepole pine and aspen were very uniform. The pine maximum ranged between 50 and 70 feet, and the aspen between 30 and 50 feet. These heights are definitely lower than would be obtained in more suitable montane habitats. It appears that both species are eventually overtopped and competitively eliminated by Douglas fir in mature forests dominated by the latter species. Additional support for this hypothesis of competitive exclusion was obtained from the DBH size-class

data.

3. Age

The oldest Douglas fir tree varied from 76 years in Stand 1B to 367 years in Stand 13J. Older trees undoubtedly occurred in these areas because diameter and age are not dependably related; also a fir in Stand 14J with a DBH of 44 inches could not be cored with the increment borer available (Table 6).

Stands 1B, 8B, 11B and 19B were even-aged and young, lacking old trees and situated in the Banff area. The maximum age of these stands was between 65 and 78 years, and the mean Douglas fir age was similarly uniform between 49 and 69 years. Single lodgepole pine in Stands 1B and 19B were exceptions, with ages of 91 and 81 years respectively. These stands also had a low standard deviation from the mean age, indicative of an even-aged condition, as well as uniformity in height as indicated in the section on height.

These data suggest that extensive fires occurred in the Banff area between 1880 and 1890. The resulting burned-over areas developed into even-aged fir and pine forests. It is possible that lodgepole pine preceded fir in some of these areas, due to the ability of pine to regenerate quickly after fire from serotinous seed sources. Douglas fir seed would have to come from outside the stand area, and/or reintroduction of fir might have been dependent

TABLE 6. AGES[a] OF TREE STRATUM COMPONENTS

Stand	*Pseudotsuga menziesii*			Effective	*Pinus contorta*	*Picea glauca*
	Mean[a]	Maximum[d]	St. Deviation	Stand Age[b]	Maximum[d]	Maximum[d]
1B	46.9	65	15.46	63.0	91	63
2B	108.9	213	67.24	185.5	86	36
3J	162.7	256	68.88	218.5	164	
4J	206.5	317	75.15	302.0	104	
5J	173.0	260	56.40	257.0	126	
6J	145.0	292	128.50	290.0	51	86
7B	169.4	290	91.79	266.0	89	72
8B	66.3	76	7.43	76.0	77	64
9B	66.5	101	17.56	89.5	66	92
10B	114.0	276	82.76	224.5	97	60
11B	69.8	78	6.08	75.5	75	71
12J	238.6	342	94.16	338.5	93	129
13J	202.7	367	107.40	345.5	58	46
14J	135.3	251	83.19	240.5	84	69
15J	181.7	195	11.97	195.0	62	
16J	157.7	224	60.60	208.5	84	61
17J	151.5	198	51.18	196.0	61	66
18J	166.1	294	68.34	248.0	57	62
19B	68.9	77	7.70	76.5	84	67
20B	111.7	194	68.00	189.0	73	57
21W	110.2	146	21.06	140.0	128	
Mean	135.9	215		201.2	86	69

NOTES:
[a] Age at DBH
[b] Mean age of oldest 25% of trees sampled
[c] Mean of all trees (over 3 inches DBH) sampled in the stand
[d] As trees were not selected for sampling on age criteria, this value will not necessarily be the oldest tree in the stand.

Plate 2 The trunk of an approximately 70 year old Douglas fir tree to show the thick fire resistant bark, and characteristic deep, vertical fissures.

on a year of abundant seed production and effective dispersal.

Isolated, very old fir trees were common in many of the stands. Large numbers of these trees were fire-scarred, indicating that their thick bark had enabled them to survive one or more fires that eliminated the smaller firs and the other three tree species. Successive fires of moderate intensity would result in a Douglas fir population clearly divisible into several age-groups. For example, the trees in Stand 20B are divisible into two groups of approximate ages 55 - 73 years and 174 - 194 years. Stands composed of several age-groups of trees tend to have large standard deviations from the mean age. Stands 6J, 13J and 14J have high standard deviations from the mean age (Table 6), and are composed of two or more age-groups of trees.

The maximum ages of lodgepole pine and white spruce varied considerably, and did not show any accord with the age of the Douglas fir except in the even-aged stands (1B, 8B, 11B and 19B). As stated above, Douglas fir was the oldest tree in all but Stands 1B and 19B. It appears that most of the white spruce (and some lodgepole pine) has become established in canopy openings or slightly more favourable habitats subsequent to the establishment of the Douglas fir majority.

Difficulty was experienced in trying to interpret the aspen increment cores due to the ill-defined nature of the annual rings. Tentative estimations based on a few

cores indicated that the maximum age of aspen rarely exceeds 60 years in habitats meeting the selection criteria.

The mean age of Douglas fir in Stand 12J was unusually large (238.6 years), resulting from poor reproduction of fir in the last 100 years. It appears that a more mesic habitat than normal for Douglas fir stands had favoured a much higher rate of establishment in white spruce than in fir.

4. Density by diameter class

The mean DBH's of Douglas fir, lodgepole pine, white spruce and aspen were 9.3, 7.0, 3.4 and 3.0 inches respectively (Table 7). All four species had a maximum density in the lowest size-class, and a progressive decrease in density with increase in size-class (Fig. 11). Density of Douglas fir trees greatly exceeded that of other tree species, except in Stand 11B where a lodgepole pine density of 3.90 trees per 100 square meters was only slightly less than the 4.15 of Douglas fir. Pine trees had a density of more than 2.0 in Stands 2B, 8B, 16J and 19B. White spruce density exceeded 2.0 only in Stands 6J and 12J. The highest density of aspen was 0.45 (Table 7).

Sapling and transgressive density showed similar trends to those of the trees, with fir usually having a far greater density than any of the other species. Important exceptions were noted in Stands 8B, 11B and 19B where the density of pine was greatest, and in Stand 12J where spruce

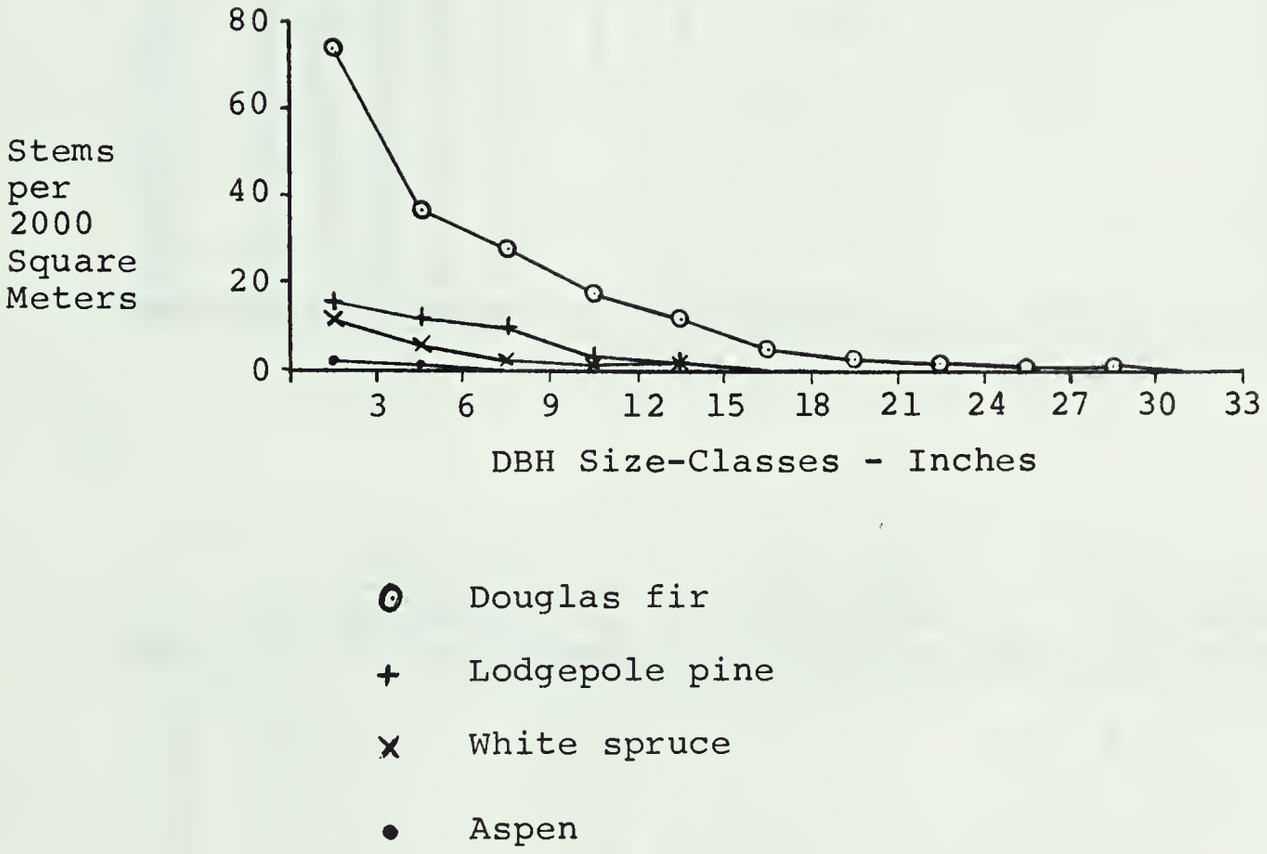


FIGURE 11. FREQUENCY POLYGONS OF THE MEAN DENSITY OF TREE SPECIES IN 3 INCH DBH SIZE-CLASSES

The densities in stems per 2000 square meters.

TABLE 7. DENSITY OF TREE SPECIES IN 3 INCH DBH SIZE-CLASSES

Expressed as stems per 2000 square meters.

Pseudotsuga menziesii

	DBH Classes - in inches													
Stand	0-3	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	27-30	30-33	33-36	36-39	Mean[a]
1B	55	46	27	14	6	1								7.0
2B	70	33	13	9	5	5	1	1						7.8
3J	140	40	14	10	7	9	2	1	1					8.5
4J	2	16	21	23	20	2		1	5			1		10.8
5J	6	14	24	27	18	15	6		1	1				11.2
6J	290	133	43	3			1	2	3	2	2			6.4
7B	17	18	19	10	19	7	6	2		4	1	1	1	12.1
8B	10	14	16	18	20	10	4							10.8
9B	52	51	44	18	4		1							7.0
10B	34	29	23	11	14	1	5		1					8.8
11B	6	27	17	23	12	4								8.7
12J	8	44	38	40	14	8	3	1		2				9.1
13J	168	42	12	6	12	11	1	1	1					8.6
14J	186	38	21	9	9	2	4	6	5	1	1			10.2
15J	35	33	52	46	22	2	1							8.8
16J	135	13	7	8	4	4	4	4	2	1	1			12.3
17J	33	33	24	12	10	7	11	9		1	1			10.9
18J	54	15	15	11	7	10	8	5	1					11.7
19B	9	17	26	27	27	7								9.9
20B	231	75	39	9	2	1	5	1						6.7
21W	10	51	86	40	18	7	6							8.5
Mean[b]	74	37	28	18	12	5	3	2	1	1				9.3

	Pinus contorta						*Picea glauca*						*Populus tremuloides*			
	DBH Classes						DBH Classes						DBH Classes			
Stand	0-3	3-6	6-9	9-12	12-15	Mean[a]	0-3	3-6	6-9	9-12	12-15	Mean[a]	0-3	3-6	6-9	Mean[a]
1B	4	5	7	3		6.9	1									
2B	23	26	14	3		5.9	7	3	1	3		7.2	1	1	1	
3J	21	13	19	1		6.3							1	2		
4J	0	1	2	2		8.1										
5J	0	2	2			6.2										
6J	1	3	11	3		7.5	92	39	14	4	1	5.8				
7B	0	1	0	2		8.5	1	0	0	0	1		1	1		
8B	80	20	22	5	1	6.7	4	2	3			4.2				
9B	1	6	8	1		6.5	1	0	0	0	2					
10B	2	1	0	4	4	11.3	1	0	1				2	8		
11B	67	31	36	9	2	6.8	17	4	4	0	1	6.8				
12J	0	0	3	4		9.2	66	57	19	4	5	6.0				
13J	24	20	7	1		5.4	3	1	1	1			7	1		
14J	15	17	3	4		5.9	9	3	0	1	1	2.2	2	7		
15J	7	17	14			5.8	3									
16J	31	30	17	3		5.9	50	17	3	1		5.2	4	3	1	
17J	5	7	5	1		6.1	3									
18J	5	12	7			5.6	1						0	1		
19B	52	35	14	4	4	6.3	1	0	1							
20B	7	11	10		1	6.3	2	1					5	6		
21W	0	0	18	7	3	8.9							15	0	1	
Mean[b]	16	12	10	3	1	7.0	12	6	2	1	1	3.4	2	1	0	3.0

NOTES: [a] Mean DBH of all trees

[b] Mean number of stems in each 3 inch size-class.

density was ten times that of the fir.

The DBH of pine and spruce reached a maximum of 15 inches. The reason for these relatively small maxima is not clear, but it is possible that the larger pine and spruce cannot tolerate interspecific competition with Douglas fir for moisture and nutrients.

Lodgepole pine had a higher mean DBH than white spruce because of its higher density in the 3 - 6 inch and 6 - 9 inch size-classes.

Inspection of the diameter size-class distribution of stands suggested recognition of four main types represented by the Frequency polygons of Stands 5J, 8B, 9B and 13J (Fig. 12).

The remaining four stands could not be grouped in any way and were treated individually.

The 0 - 3 inch size-class includes all transgressives and saplings but not seedlings.

Type 1 = Stand 13J (representing Stands 2B, 3J, 14J, 18J and 20B).

This polygon shows two distinct peaks in size-class. A feature of the smaller diameter peak (0 - 6 inches), is the very high density of Douglas fir saplings and transgressives; pine is well represented but spruce and aspen are sporadic. The larger diameter peak (12 - 18 inch) is exclusively Douglas fir. It appears that this type of forest is composed of a basic 'skeleton' of medium

FIGURE 12. FREQUENCY POLYGONS OF THE DENSITIES OF TREE SPECIES IN 3 INCH DBH SIZE-CLASSES FOR INDIVIDUAL STANDS

The densities in stems per 2000 square meters.

⊙ Douglas fir

\+ Lodgepole pine

× White spruce

• Aspen

(a) Type 1 (Stand 13) and representing Stands 2, 3, 14, 18 and 20

(b) Type 2 (Stand 9) and representing Stands 1, 10, 15 and 17

(c) Type 3 (Stand 8) and representing Stands 11 and 19

(d) Type 4 (Stand 5) and representing Stands 4 and 7

(e) Stand 12

(f) Stand 16

(g) Stand 6

(h) Stand 21

FIGURE 12

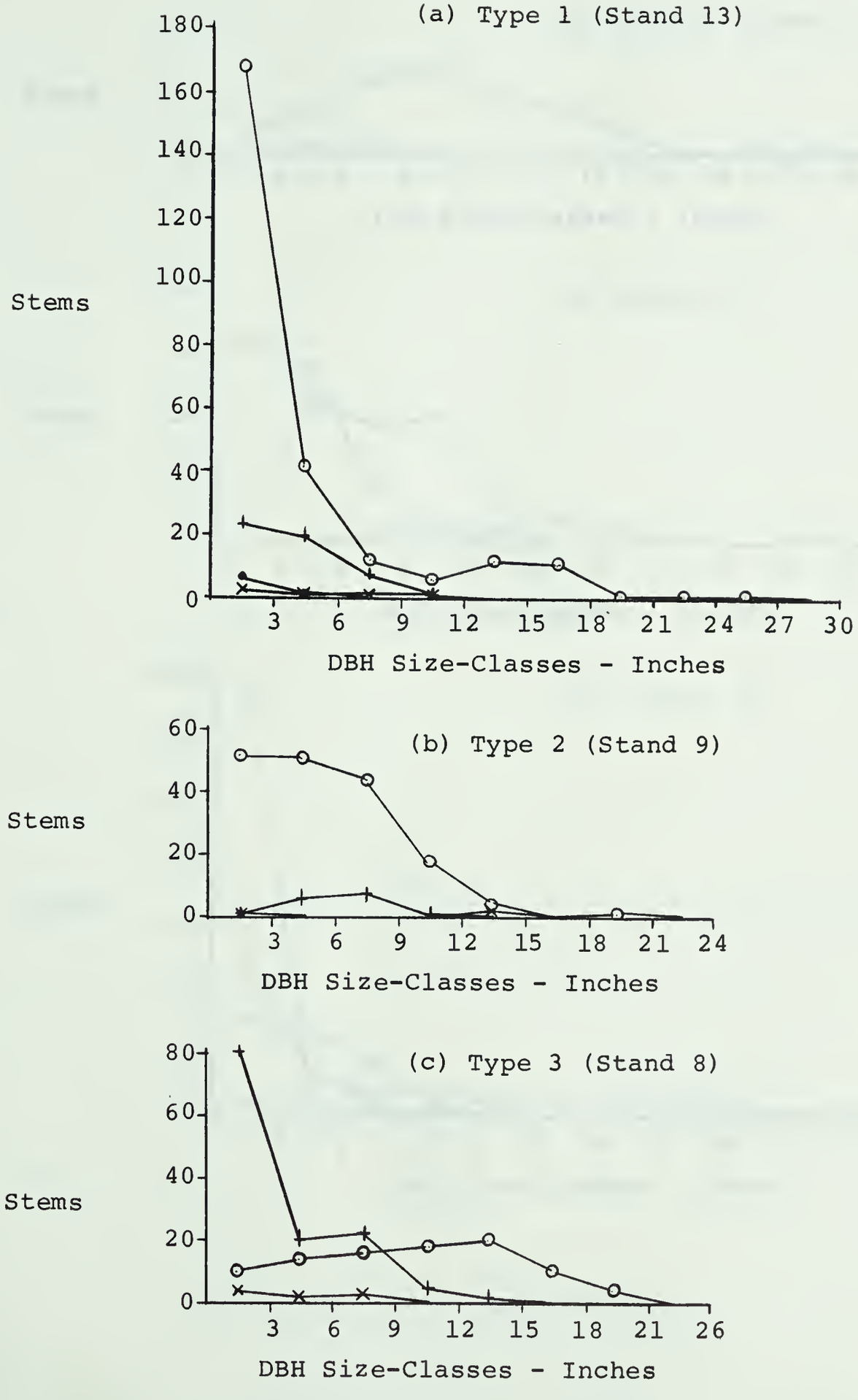
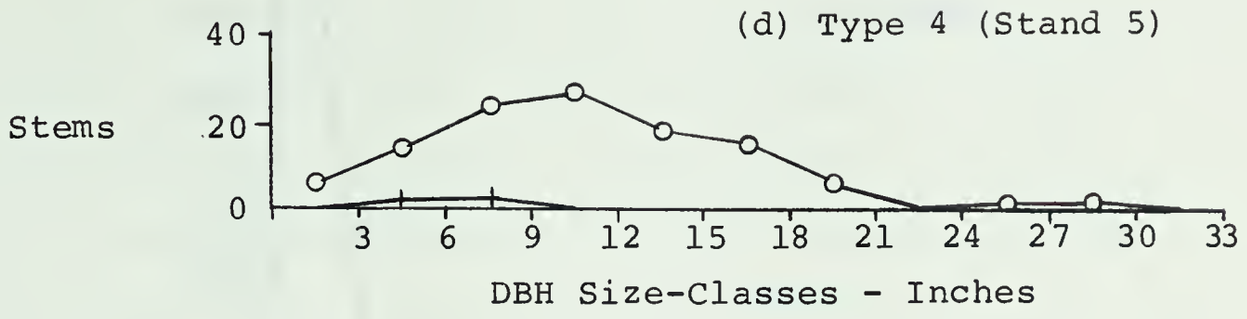
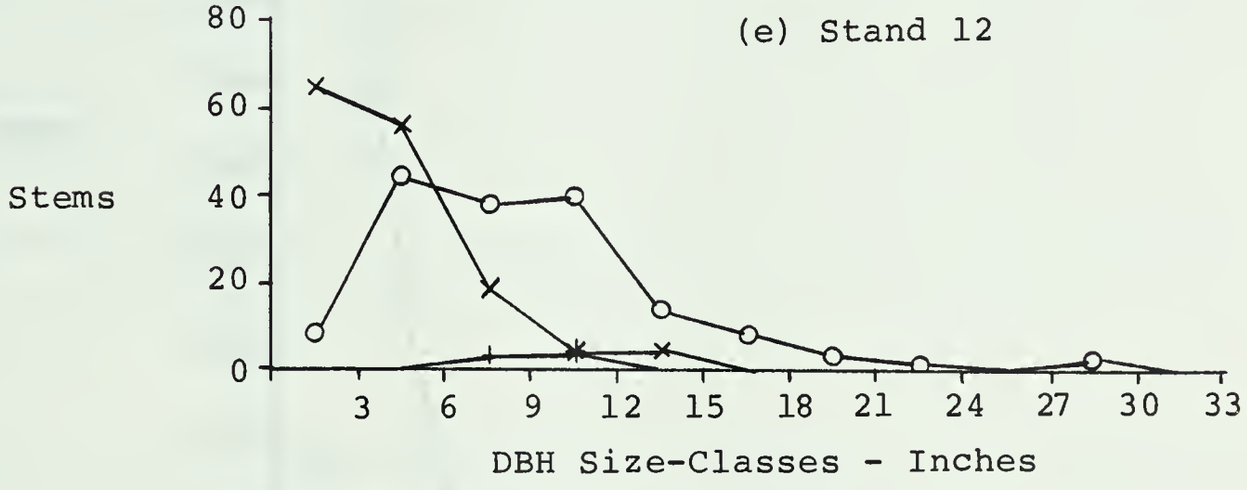
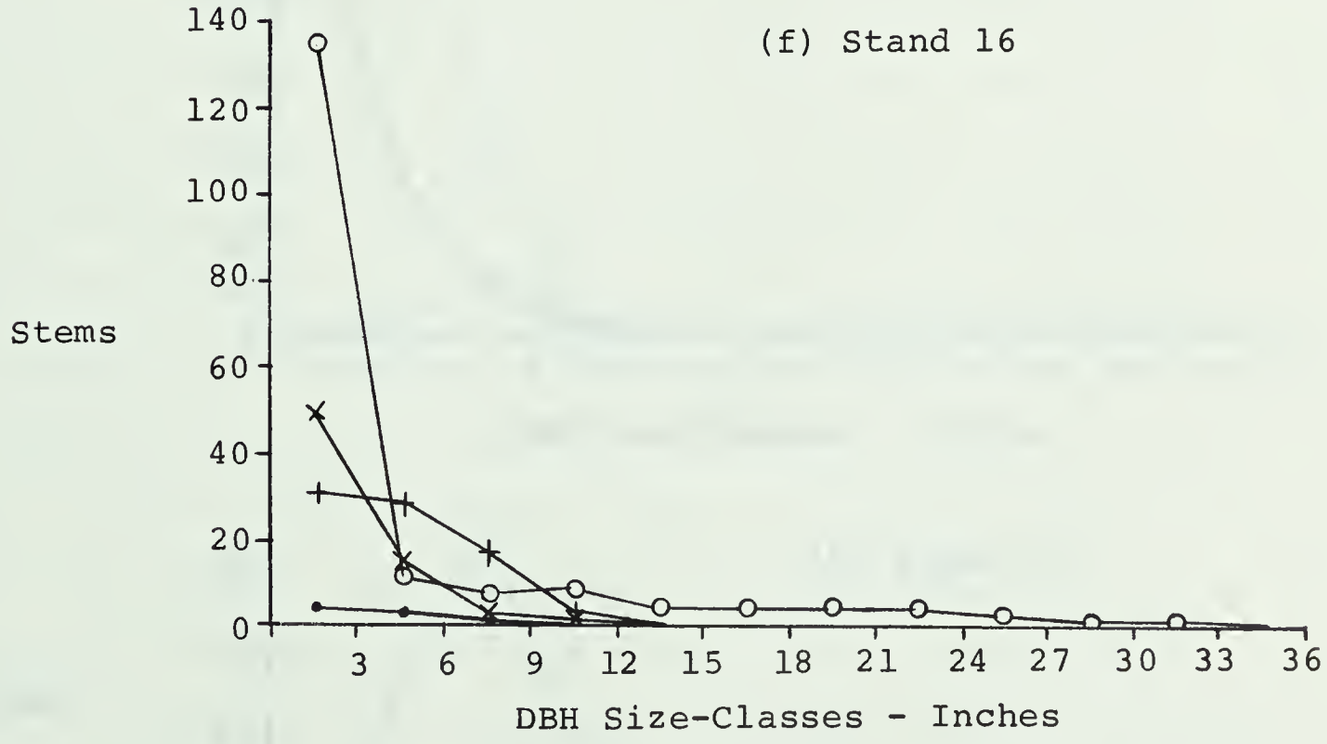
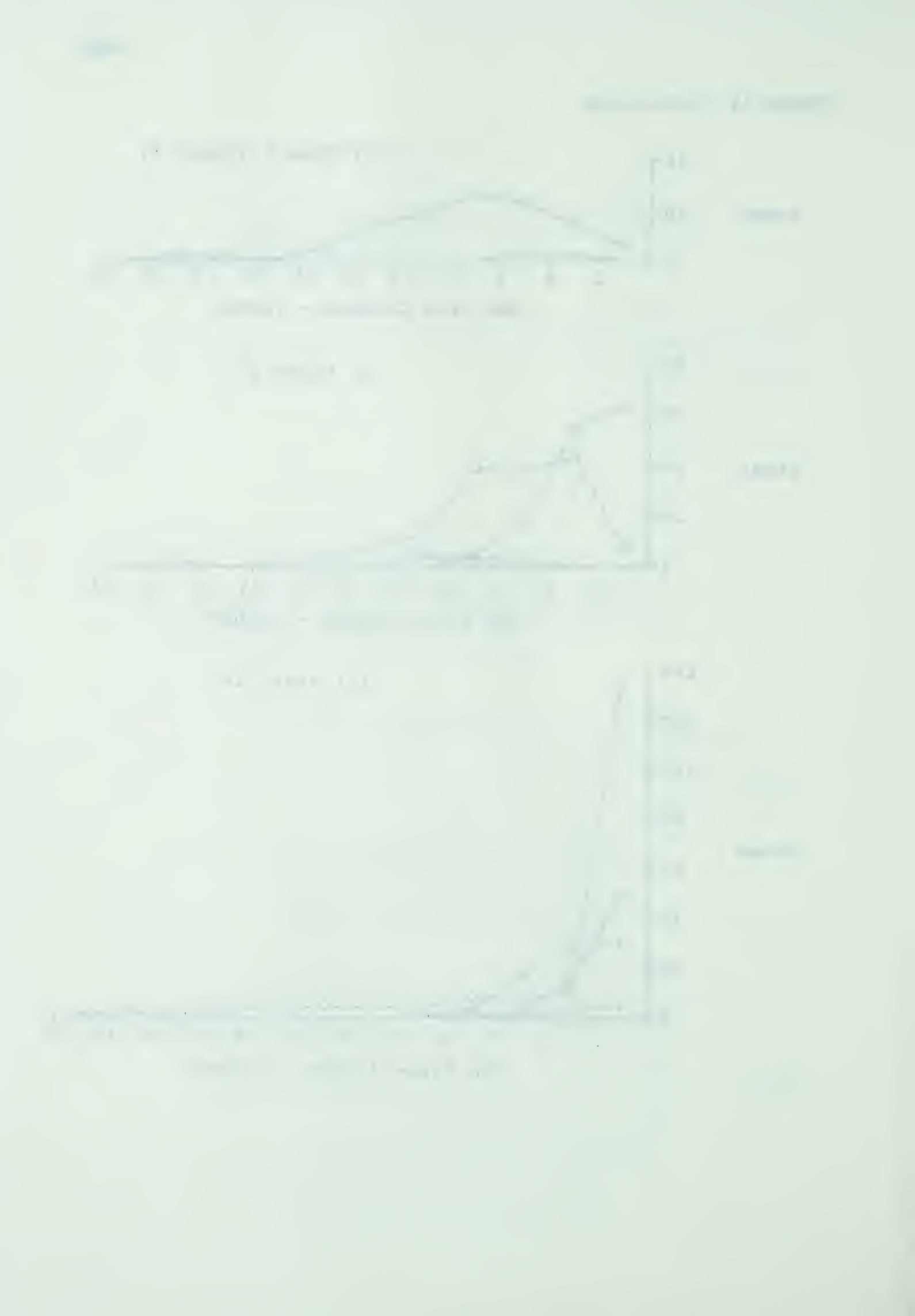

(a) Type 1 (Stand 13)
Stems
180
160
140
120
100
80
60
40
20
0
3 6 9 12 15 18 21 24 27 30
DBH Size-Classes - Inches
(b) Type 2 (Stand 9)
Stems
60
40
20
0
3 6 9 12 15 18 21 24
DBH Size-Classes - Inches
(c) Type 3 (Stand 8)
Stems
80
60
40
20
0
3 6 9 12 15 18 21 26
DBH Size-Classes - Inches

FIGURE 12 (continued)









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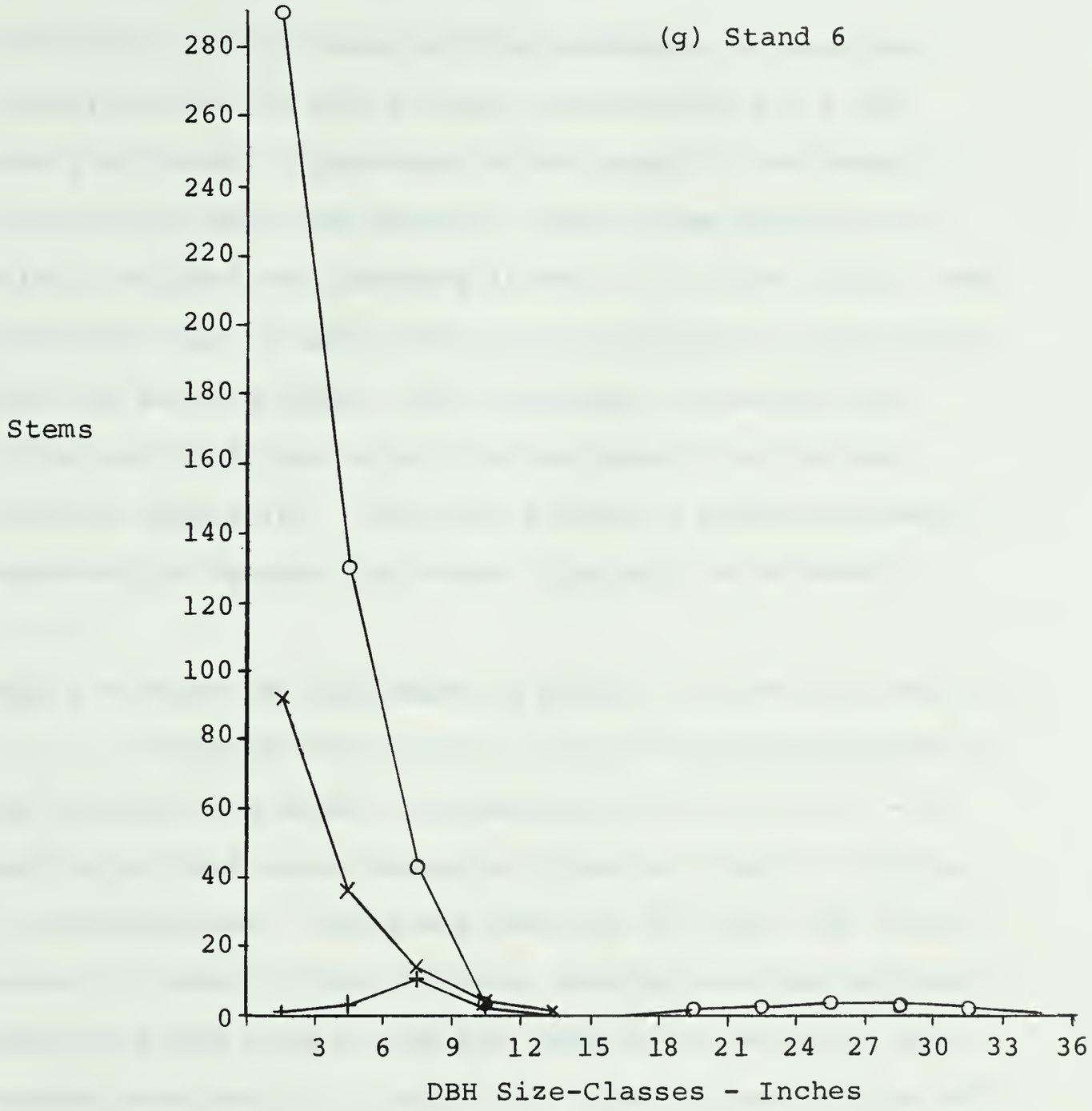
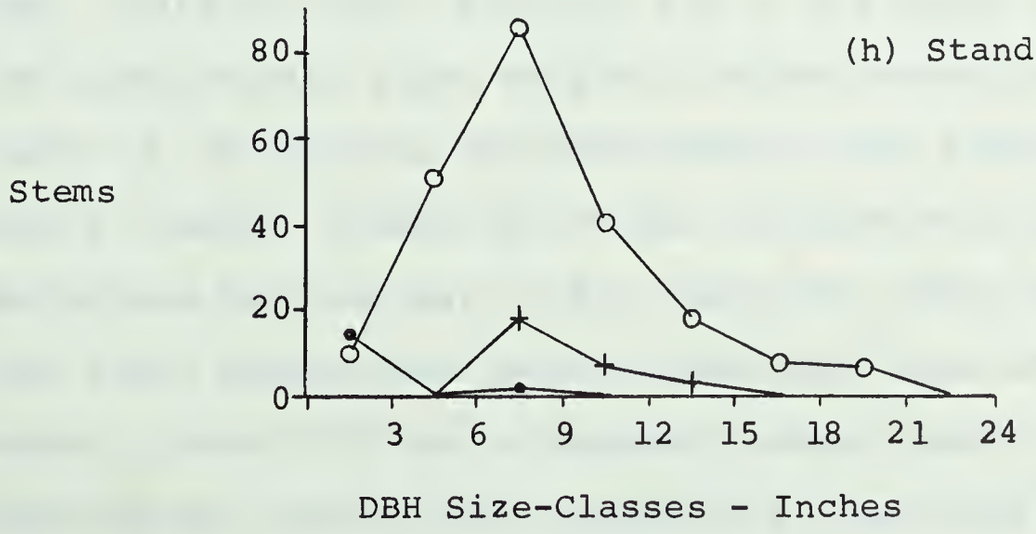
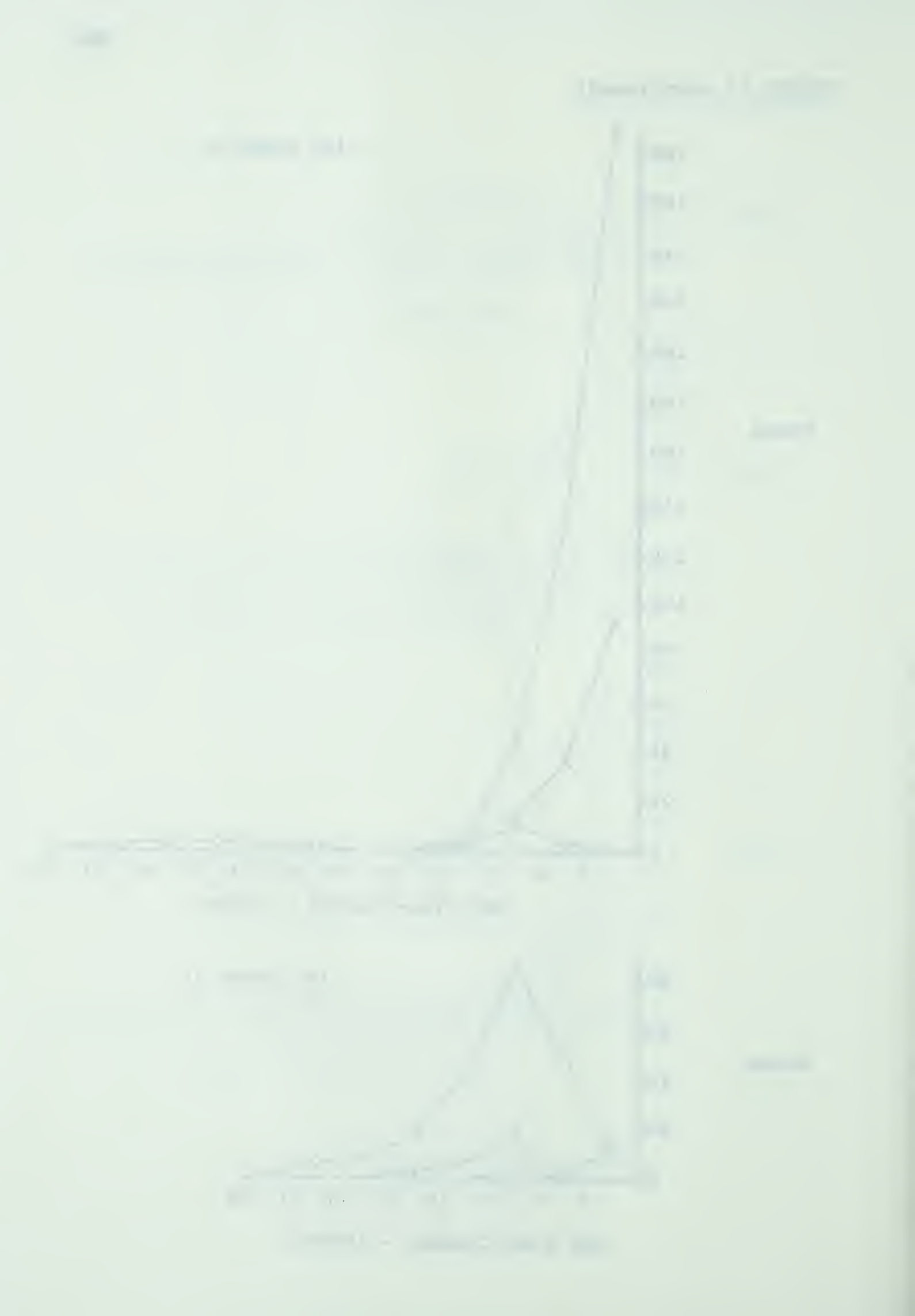






-to-large size fir trees with an abundance of saplings, transgressives and small trees, predominantly fir and mostly situated in openings in the canopy. Few trees of intermediate size are present. Other tree species are mainly confined to diameters in the 0 - 6 inch range. The hypothesis can be made that this distribution type results from one or more fires, that destroyed all except the larger and therefore more fire-resistant firs in the original population. The fire allowed a sudden increase in reproduction beneath the canopy openings so produced.

Type 2 = Stand 9B (representing Stands 1B, 10B, 15J and 17J)

Douglas fir in the 0 - 9 inch size-range make up the bulk of this stand, the density of fir in the 6 - 9 inch size-class being almost as great as that of saplings + transgressives. There are very few fir with DBH values above 12 inches. Trees of other species are few and small. Although these five stands are composed of uniform, small -to-medium-sized fir, there is no apparent correlation with age. Stand 15J has a mean fir age of 182 years, many of the trees showing signs of slow, stunted growth, whereas stand 1B is vigorous and fast-growing with a mean age of only 47 years. Stands 1B, 9B and 15J have very low standard deviations for mean age of fir (Table 6), which suggests that their populations became established soon after fire. Stands 10B and 17J have a somewhat larger range of tree size and age, having small numbers of trees with DBH values

over 20 inches and ages up to 276 years.

Type 3 = Stand 8B (representing Stands 11B and 19B)

This frequency polygon is characterized by the completely different size-class distributions of the two major species, lodgepole pine and Douglas fir. The fir is evenly-distributed over a range of 3 - 15 inch DBH, with the density in any one class never exceeding 27 stems per 2000 square meters. Few transgressives or saplings are present, and there are no trees with DBH values over 21 inches.

Pine, however, is restricted to the smaller size -classes, reaching highest density of 80 stems in the 0 - 3 inch size-class. Stand 11B has a considerable number of spruce in the 0 - 9 inch range, and it seems likely that, in this stand and to a lesser extent Stand 8B, local environmental conditions or recent historical events were less favourable to the reproduction of fir than pine and spruce.

Type 4 = Stand 5J (representing Stands 4J and 7B)

The density of fir reaches a peak at about 10 inches DBH, the density decreasing steadily for smaller and larger size-classes. A few scattered, very large fir with DBH values up to 39 inches are present. These three stands have relatively high, continuous canopies, and reproduction of all species is very sparse. Trees of other

species are almost entirely absent.

It is possible to look upon these groups of stands as different stages in a maturation cycle of Douglas fir. Starting with Type 1 (large reproduction and small trees, with a smaller number of scattered large fir), and progressing through Type 2 to the closed canopy, mature forest of Type 4, forms a series or reproduction cycle. The closed canopy of Type 4 will eventually break down, allowing patches of reproduction and the cycle will be complete. The other four stands and Type 3 do not fit this cycle because of their relatively large densities of pine and spruce. It is possible that Type 3 represents an interruption in the normal cycle due to fire.

Stand 16J

This frequency polygon is very similar to Type 1, to which the same remarks apply, except that there are a large number of white spruce present in the 0 - 6 inch DBH range. This is probably a reflection of the topography, for the aspect of this stand was northwest, resulting in a more mesic habitat than normal for a Douglas fir stand in this region.

Stand 6J

The sapling and transgressive density of both fir and spruce is exceptionally high. A few very large

Douglas fir produce a markedly disjunct size-class distribution. The small pine population reaches a peak in the 6 - 9 inch size-class, the size at which the populations of spruce and fir were declining sharply. This is highly indicative of a fire subsequent to which the pine reproduction was most rapid.

Stand 12J

In this stand white spruce reproduction is far greater than fir, resulting in domination of the 0 - 6 inch size-class by spruce. This trend is reversed as the size increases. All the larger trees in the stand (over 15 inch DBH) were fir. There were strong signs that spruce was succeeding fir, and like Stand 16J the habitat seemed more mesic than normal for Douglas fir.

Stand 21W

The size distribution of fir reaches a strong peak in the 6 - 9 inch class, which is also the peak density of the smaller pine populations. Very few large trees are present and very little reproduction is taking place. The uniformity in age, height and size of the tree stratum points strongly to simultaneous invasion by pine and Douglas fir following fire over 100 years ago.

An attempt was made to interpret these DBH size-classes in terms of age, but a good correlation between

age and DBH of trees could not be found. A slight trend was noted, but too many exceptions to the general rule of age proportionate to DBH were found to be of practical value.

5. Basal area

Basal area was the most useful single attribute of the tree stratum for which data were obtained in this study. It gave a good estimation of the proportion of ground surface occupied by stems of each species, and was a useful means of comparing their importance. The mean basal area of each species in all stands was: Douglas fir, 111.7; lodgepole pine, 16.1; white spruce, 4.7; and aspen, 0.6 square feet per acre, and their standard deviations were 38.7, 14.4, 11.5 and 0.8 respectively (Table 8). The standard deviation of spruce was almost three times the mean basal area, indicating that this species occurs only sporadically in the mature phase of the Douglas fir ecosystem. Lodgepole pine was present in all stands but only in Stand 11B did its basal area (60.5 square feet per acre) come close to that of the Douglas fir (84.0). Although the basal area of pine was second only to fir in 19 of the 21 stands, its mean and standard deviation suggest that lodgepole pine plays a constant but relatively minor role in mature stands of the Douglas fir ecosystem.

The basal area of aspen was very small with a maximum value of only 2.4 in Stand 10B. These basal area values demonstrate, better than any other single variable,

TABLE 8. BASAL AREA OF TREES BY SPECIES

Expressed in square feet per acre.

Stand	*Pseudotsuga menziesii*	*Pinus contorta*	*Picea glauca*	*Populus tremuloides*	Other species	Total
1B	54.3	10.7	0.7			65.7
2B	42.7	22.3	2.3	1.3		68.7
3J	79.1	19.1		1.2		99.4
4J	153.5	3.5	0.5			157.5
5J	149.5	1.0				150.5
6J	102.5	13.5	14.5	1.5		132.0
7B	150.8	1.2	0.8	1.7		154.5
8B	98.0	28.0	2.5			128.5
9B	91.5	15.0	1.5			108.0
10B	86.4	12.8		2.4		101.6
11B	84.0	60.5	6.0			150.5
12J	184.5	1.5	51.0		0.5[a]	237.5
13J	98.3	18.3	0.3	1.0		117.9
14J	128.0	7.5	4.5	1.0		141.0
15J	152.5	15.5				168.0
16J	75.0	28.3	7.3	1.7		112.3
17J	166.0	6.0	2.0			174.0
18J	112.3	9.1				121.4
19B	133.0	38.0				171.0
20B	92.0	10.0	0.5	1.5		104.0
21W	215.0	26.0		0.5	1.0[b]	242.5
Mean	111.7	16.1	4.7	0.6		133.2
St. Deviation	38.7	14.4	11.5	0.6		39.8

NOTES: [a] *Betula papyrifera*

[b] *Abies lasiocarpa.*

that Douglas fir can completely dominate parts of the montane zone in Banff and Jasper, for it accounted for 84% of the total basal area of all stands sampled.

6. Cover

The cover of individual tree species was calculated from the point quadrat data (Table 9), whereas the vertical photograph method was thought to give the more accurate estimation of total tree canopy cover.

Tree canopy cover varied from a minimum of 27.5% in Stand 11B to a maximum 64.2% in Stand 5J. Stand 21W had a cover of 74.7% derived from the point quadrat method, but no vertical photographs were taken at Waterton.

There was some evidence that a high proportion of lodgepole pine in stands was associated with a comparatively low total canopy cover (Stands 2B, 11B and 16J). Pine tends to have a smaller cover per tree than does fir or spruce.

Spruce had a high cover value only in Stand 12J (17.2%); its mean cover for all stands was only 1.7%, compared with 5.3% for pine and 42.3% for Douglas fir. Aspen, with a mean of 0.7% had a very minor role in the total canopy cover, due to its low density and diffuse foliage.

7. Tree reproduction

The mean Frequencies of Douglas fir saplings, transgressives and seedlings were 44, 42 and 28% respectively (Table 11). No comparisons between these values are valid

TABLE 9. PERCENTAGE COVER OF TREE AND SHRUB STRATA AND THEIR MAJOR SPECIES

Includes only those species with both a mean cover of 0.5% or over, and a presence value of 20% or over.

Species	Stands																					
	Banff									Jasper											Waterton	
	1	2	7	8	9	10	11	19	20	3	4	5	6	12	13	14	15	16	17	18	21	Mean
Trees																						
Pseudotsuga menziesii	34.1	21.1	55.6	36.1	38.3	36.9	20.0	37.8	44.9	40.1	49.4	57.2	57.8	46.7	45.2	53.9	45.5	25.5	60.5	38.8	65.5	42.3
Pinus contorta	4.4	5.9	0.9	7.2	4.4	4.4	20.5	10.6	2.8	4.7	1.7	1.1	5.5	0.5	6.7	3.3	6.1	7.8	1.1	6.1	8.3	5.3
Picea glauca		0.4	0.5	0.5	0.5		2.2						7.2	17.2	0.4	1.1		3.7				1.7
Populus tremuloides		1.1	1.4			1.3	0.5		2.2	1.3			2.8		0.4	2.8		0.4		0.5	0.5	0.7
Total Tree Cover	38.5	28.5	58.4	43.8	43.2	42.6	43.2	48.4	49.9	46.1	51.1	58.3	73.3	64.4	52.7	61.1	51.6	37.4	61.6	45.4	74.3	51.1
Tree Cover From Vertical Photographs	31.0	36.0	53.3	41.0	54.5	44.0	27.5	59.0	36.5	35.5	48.5	64.2	54.4	47.7	39.7	44.0	52.0	35.7	61.5	42.7	-[a]	45.4
Shrubs																						
Juniperus communis	5.2	14.3			3.8	1.8	0.2	3.2	6.8	0.2			0.2	0.8				1.3	1.5			2.0
Rosa acicularis	0.3	0.3	0.8	0.8			0.2	0.2	0.5	0.5	1.2		2.8	2.0	2.0	4.8		2.3	0.5	0.5	0.2	1.0
Shepherdia canadensis	0.2	1.8		0.5	0.5	0.8	0.2	0.2	1.5	0.2	0.2		2.2		3.0	1.5	1.2	2.8	0.2	0.7		0.9
Total Shrub Cover	11.3	20.3	0.8	1.3	8.7	3.0	1.4	3.8	12.3	1.1	2.2		7.2	3.0	6.8	8.3	1.4	7.6	2.4	1.2	20.4	5.9

NOTES: [a] No observations made.

TABLE 10. QUADRAT FREQUENCY PERCENTAGES FOR SPECIES OF THE TREE AND SHRUB STRATA

Includes only those species with a mean frequency of 10% or over and a presence value of 20% or over; 10x10 meter quadrats for trees, 4x4 meter quadrats for shrubs.

	Stands																					
	Banff									Jasper										Waterton		
Species	1	2	7	8	9	10	11	19	20	3	4	5	6	12	13	14	15	16	17	18	21	Mean
Trees																						
Pseudotsuga menziesii	100	97	100	100	100	92	95	100	100	100	95	100	100	100	100	100	100	100	100	95	100	99
Pinus contorta	30	73	12	80	50	28	95	65	60	48	10	15	40	10	43	50	20	73	30	32	55	43
Picea glauca		30	4	25	5	4	40	5	5				80	90	10	10		40				17
Populus tremuloides		13	4			8			20	6			25		3	25		13		4	5	6
Shrubs																						
Rosa acicularis	20	40	33	100	60	40	65	95	70	39	80	10	95	85	97	100	40	90	25	54	35	62
Shepherdia canadensis	53	63	4	60	45	32	55	40	65	30	30	5	60	25	53	75	45	97	20	36		45
Spiraea lucida		70	25	75	55	68	100	100	85		25		35		53	40	25	83	55		80	45
Juniperus communis	50	80	4	30	55	12	25	20	45	6			15	10			10	17	10	4		20
Symphoricarpos albus	50	13		5	20	8		10	25	12	30		80	65		5				14	70	17
Amelanchier alnifolia	57	7			10			20	55	3	10		5	15	40	10				14	40	12

TABLE 11. QUADRAT FREQUENCY PERCENTAGES OF SAPLINGS, TRANSGRESSIVES AND SEEDLINGS OF TREE SPECIES

Sizes of quadrats used were 10x10 meters for saplings, 4x4 meters for transgressives and 1x1 meter for seedlings.

	Pseudotsuga menziesii			*Pinus contorta*			*Picea glauca*			*Populus tremuloides*		
Stand	Sap.	Trans.	Seed	Sap.	Trans.	Seed	Sap.	Trans.	Seed	Sap.	Trans.	Seed
1B	73	37	13	17	3		3					
2B	67	33	17	27	30		13	7	3		17	3
3J	64	61	24	21	9					3	9	
4J	10	20	35									
5J	5	5	45									
6J	100	90	35	5			85	50		15		5
7B	21	21					4			4	12	
8B	30	20	50	55	60		15	5			10	
9B	60	65		5				5				
10B	44	40		8				4		4	4	
11B	20	5	50	75	55		20	35	5			
12J	30	10	40		50		75	15	15			
13J	67	83	50	23	13		10	7		10	7	
14J	65	75	65	20	10		10	5		5		
15J	15	30	15	15	10		15					
16J	47	83	43	33	33		47	20		10	13	3
17J	45	40	25	5			5	10				
18J	41	46	32	14	5		5				5	
19B	15	20	25	55	45		5				5	
20B	90	100	5	20	5		10			15	30	5
21W	25		20							10	15	
Mean	44	42	28	19	16		15	8	1	4	6	1

TABLE 12. DENSITY OF LIVING TREES, SAPLINGS AND TRANSGRESSIVES

Expressed as stems per 100 square meters.

Stand	*Pseudotsuga menziesii*			*Pinus contorta*			*Picea glauca*			*Populus tremuloides*			Total Tree Density
	Trees	Sap.	Trans.	Trees	Sap.	Trans.	Trees	Sap.	Trans.	Trees	Sap.	Trans.	
1B	4.73	2.10	0.63	0.73	0.17			0.03					5.46
2B	3.33	2.23	1.27	2.13	0.60	0.57	0.37	0.20	0.13	0.13		0.03	5.96
3J	4.15	3.27	3.73	1.64	0.96	0.09				0.12	0.03		5.91
4J	4.45	0.10		0.25									4.70
5J	5.30	0.20	0.10	0.20									5.50
6J	9.45	7.60	6.90	0.85	0.05		2.90	3.00	1.60	0.30	0.15		13.50
7B	4.42	0.63	0.21	0.12			0.04	0.04		0.04	0.04		4.62
8B	4.10	0.30	0.20	2.40	1.70	2.30	0.25	0.15	0.05				6.75
9B	5.90	1.50	1.10	0.75	0.05		0.10		0.05				6.75
10B	4.20	1.00	0.72	0.44	0.08		0.04		0.04	0.40	0.12		5.08
11B	4.15	0.20	1.00	3.90	2.05	1.30	0.45	0.20	0.65				8.50
12J	7.50	0.40		0.15			4.25	2.30	1.00				11.95[a]
13J	4.30	4.03	4.37	1.40	0.97	0.23	0.10	0.10	0.07	0.03	0.23	0.13	5.83
14J	4.80	3.35	5.95	1.20	0.50	0.25	0.25	0.40	0.05	0.35	0.10		6.60
15J	7.80	0.45	1.30	1.55	0.25	0.10		0.15					9.35
16J	2.47	1.20	5.53	2.50	0.90	0.63	1.07	1.70	0.80	0.20	0.17	0.03	6.24
17J	5.40	1.05	0.60	0.65	0.25			0.05	0.10				6.05
18J	3.59	1.32	1.36	0.95	1.82	0.45		0.45		0.45			4.99
19B	5.20	0.15	0.30	2.85	1.20	1.40	0.05	0.05					8.10
20B	6.60	6.15	5.40	1.10	0.30	0.05	0.05	0.10	0.05	0.30	0.20		8.05
21W	10.40	0.50		1.40						0.05	0.15	0.60	11.95[b]
Mean	5.09	1.86	1.94	1.29	0.59	0.35	0.50	0.42	0.22	0.12	0.06	0.04	6.99
St. Dev.	1.66	2.08		0.95	0.66		1.10			0.16			2.35

NOTES: [a] Includes a density of 0.05 for *Betula papyrifera*

[b] Includes a density of 0.10 for *Abies lasiocarpa*.

TABLE 13. DENSITY OF DEAD TREES AND SAPLINGS

Expressed in stems per 100 square meters.

Stand	*Pseudotsuga menziesii*		*Pinus contorta*		*Picea glauca*		*Populus tremuloides*	
	Trees	Saplings	Trees	Saplings	Trees	Saplings	Trees	Saplings
1B			0.20	0.20				
2B	0.13	0.10	0.50	0.23	0.13		0.67	0.03
3J	0.09	0.30	0.06	0.18			0.03	
4J	0.10	0.10	0.05					
5J	0.15	0.25	0.05					
6J	0.55	2.90			0.10	0.40	0.60	2.45
7B		0.12						
8B	0.15	0.15						0.25
9B	0.10	0.05	0.15				0.25	1.20
10B		0.04	0.08				0.24	0.24
11B	0.05	0.05	0.25	0.75			0.05	0.70
12J	0.30	0.30			0.40	0.95		
13J	0.13	0.20	0.03	0.07			0.03	0.10
14J		0.10					0.05	0.15
15J	0.80	0.05	0.15	0.10				
16J		0.03	0.23	0.17			0.20	0.20
17J	0.05	0.05	0.15	0.05				
18J	0.27		0.15					
19B	0.10	0.20	0.15	0.20			0.10	
20B		0.50					0.65	0.70
21W	4.20	1.95	0.40					
Mean	0.34	0.35	0.12	0.09	0.03	0.06	0.14	0.29

as different-sized quadrats were used in sampling: 10 x 10 meters for sapling, 4 x 4 meters for transgressive and 1 x 1 meters for seedling Frequency. Frequency increases with increasing sampling quadrat size (Oosting 1956, pp. 60-61), so that the mean Frequency of Douglas fir seedlings might have been greater than the sapling Frequency if sampled with equal -sized quadrats.

Several stands had a low density of fir transgressives and saplings (Stands 4J, 5J, 7B, 8B, 12J, 19B and 21W; Table 12). All of these tended to have high mean values for total basal area and tree cover, suggesting that environmental factors such as light, soil moisture or available nutrients could be limiting to reproduction because of competition with the tree stratum. Conversely, however, those stands with low basal area and tree cover values do not necessarily have a high reproductivity because other factors such as steep slopes or heavy shrub cover, limiting to both tree productivity and reproduction, come into play.

Lodgepole pine seedlings were either absent or very rare in all stands. Saplings and transgressives of pine were also very sparse, except in Stands 8B, 11B, 16J and 19B where many of them showed poor, etiolated growth. It is therefore probable that much pine reproduction consisted of retarded specimens with very slow growth rates. The four exceptions to this generalization were stands with a comparatively high proportion of pine in the canopy. On the whole, the theory that successful pine seedling estab-

lishment usually occurs only after disturbances such as fire is supported by these data.

Aspen reproduction was very poor in all stands, and white spruce reproduction was common only in Stands 6J, 12J and 16J, three stands having a relatively high proportion of spruce in the canopy.

The density of the transgressives and saplings of all four species was lower than that of the trees. The few exceptions emphasize that reproductive stages were poorly represented in the mature phase of the Douglas fir ecosystem in Banff and Jasper, for all four tree species.

With the exception of aspen, the mean density of dead saplings was low compared with living saplings (Table 13), and a similar relationship existed between dead and living trees. This indicates that large scale thinning out of reproductive stages, due to mutual competition, rarely occurs in these stands, and that, with the exception of aspen, the critical stage in reproduction occurs before development has progressed beyond the transgressive stage of the life cycle.

The density of dead aspen was greater than live aspen at both the tree and sapling stages. This species was usually found in isolated thickets or clumps, situated in gullies of stands, where the moisture relations were locally improved. It was evident that browsing, probably by elk or mule deer, was the probable cause of this large ratio of dead-to-living aspen, rather than mutual or interspecific

competition.

8. Frequency

Douglas fir occurred in all quadrats in 16 stands, and had a minimum of 92% Frequency in Stand 10B (Table 10). This indicates that fir populations were uniformly dispersed in most of the stands, although different size-class groups may form clumps or aggregates.

Lodgepole pine, with a Frequency between 10% in Stands 4J and 12J, and 95% in Stand 11B, had a high mean Frequency of 43%. This mean value is relatively high for a species with a low density and basal area, and would seem to indicate that pine is widely and fairly-evenly distributed. However, data on the dispersion pattern of the tree stratum (p. 106) seem to contradict this conclusion. A hypothesis to explain this apparent contradiction will be found on page 106.

The Frequency of white spruce varied from 90% in Stand 12J to nil in 8 stands, and had a comparatively low mean of 17%.

Aspen, too, had a wide range of Frequencies (0 - 25%), and a comparatively low mean of 6%. Both these species (spruce and aspen) had high Frequencies in a few stands only, indicating that they were of sporadic occurrence in the mature phase of the Douglas fir ecosystem.

Dispersion Pattern of the Tree Stratum

Blackman's Coefficient of Dispersion Method

This method of assessing dispersion pattern (Blackman, 1942), based on the equality of the variance and mean of a Poisson distribution, was applied to the density of tree populations. It was assumed that the density of trees was not so great as to preclude comparison of its distribution with that of Poisson expectation. If the density were to approach the maximum possible under the physical limitations of the environment, then a binomial expectation would be more appropriate, and this test would not be valid.

The variance-to-mean ratio (coefficient of dispersion) (Greig-Smith, 1964, p. 63) was calculated for total tree density, Douglas fir population density and densities of other species populations for each stand. It was decided not to apply this test to species with a density of less than one stem per 100 square meters, as these could little effect the dispersion pattern of the tree stratum as a whole. Also, the sampling estimations of density for these minor species was inadequate. A variance-to-mean ratio of more than one is indicative of a variance greater than random expectation, and a clumped or contagious distribution. Similarly, a variance-to-mean ratio of less than one indicates a regular or uniform pattern. The significance of any departure from random dispersion was tested by calculating an index of dispersion,

and referring it to the table of Chi-square with degrees of freedom one less than the number of observations (Snedecor, 1956, pp. 28-29).

$$\text{Index of Dispersion} = \frac{\text{Variance}}{\text{Mean}} \times N-1$$

where N = number of observations.

A result of significant contagion with this method would indicate that comparing the density data with Poisson expectation was valid, and that the density of trees was not close to the maximum possible. A density approaching the maximum would tend to have a regular distribution due to maximum exclusion. The assumption has to be made that the area of the stand is equally able to support the development of a tree stratum. In some stands this may not be true, and so the detection of a contagious distribution in an environment including areas not suitable for tree growth does not irrefutably substantiate the validity of Poisson expectation.

The 10 x 10 meter quadrat was thought to be adequate to sample the tree stratum (p. 50), but the detection of non-randomness with this method would be indicative of pattern for that size of quadrat only (Kershaw, 1964, p. 104).

The following results were obtained with this test (Table 14). Douglas fir was contagiously distributed in eight stands (No. 1B, 2B, 6J, 10B, 13J, 15J, 20B and 21W)

TABLE 14. WITHIN-STAND DISTRIBUTION PATTERN IN THE TREE STRATUM

From density data (TABLE 12) using coefficient of dispersion (page 102) and 5% significance level.

Species	Stand	Number of Observations	Degrees of Freedom	Variance	Coefficient of Dispersion	Index of Dispersion	Pattern[a]
Total Trees	1B	30	29	15.50	2.82	81.72	C
	2B	30	29	9.91	1.62	46.89	C
	3J	33	32	11.57	1.98	63.30	C
	4J	20	19	7.91	1.68	43.02	C
	5J	20	19	3.99	0.69	13.19	R
	6J	20	19	19.52	1.45	27.59	R
	7B	24	23	4.59	0.99	22.79	R
	8B	20	19	9.48	1.42	26.89	R
	9B	20	19	7.85	1.15	21.93	R
	10B	25	24	7.99	1.57	37.75	C
	11B	20	19	8.66	1.00	19.02	R
	12J	20	19	14.37	1.20	22.84	R
	13J	30	29	8.63	1.48	42.92	C
	14J	20	19	7.52	1.14	21.64	R
	15J	20	19	8.56	0.92	17.38	R
	16J	30	29	9.77	1.59	46.24	C
	17J	20	19	5.84	0.97	18.34	R
	18J	22	21	2.68	0.54	10.28	R
	19B	20	19	7.92	0.97	18.47	R
	20B	20	19	11.31	1.41	26.69	R
	21W	20	19	18.62	1.54	29.24	R
Pseudotsuga menziesii	1B	30	29	12.34	2.61	75.61	C
	2B	30	29	7.01	2.06	59.76	C
	3J	33	32	3.48	0.85	27.06	R
	4J	20	19	6.16	1.38	26.28	R
	5J	20	19	4.37	0.79	14.95	R
	6J	20	19	24.89	2.63	50.05	C
	7B	24	23	4.52	1.02	23.51	R
	8B	20	19	1.78	0.43	8.24	U
	9B	20	19	4.37	0.73	13.94	R
	10B	25	24	7.42	1.77	42.38	C
	11B	20	19	4.03	0.97	18.45	R
	12J	20	19	11.95	1.58	30.06	R
	13J	30	29	5.96	1.48	42.89	C
	14J	20	19	6.48	1.35	25.67	R
	15J	20	19	12.38	1.59	30.15	C
	16J	30	29	2.67	1.07	31.00	R
	17J	20	19	3.41	0.63	12.00	R
	18J	22	21	2.92	0.81	17.08	R
	19B	20	19	7.64	1.47	27.92	R
	20B	20	19	11.52	1.75	33.15	C
	21W	20	19	22.05	2.11	40.09	C
Pinus contorta	2B	30	29	5.13	2.33	67.60	C
	3J	33	32	6.31	3.92	125.40	C
	8B	20	19	7.10	2.90	55.08	C
	11B	20	19	3.16	0.79	15.00	R
	13J	30	29	6.09	3.65	105.75	C
	14J	20	19	5.33	4.45	84.40	C
	15J	20	19	12.37	7.98	151.50	C
	16J	30	29	4.94	2.03	58.93	C
	19B	20	19	11.57	3.98	75.66	C
	20B	20	19	1.46	1.33	25.30	R
	21W	20	19	2.78	1.98	37.71	C
Picea glauca	6J	20	19	6.77	2.37	45.10	C
	12J	20	19	9.78	2.30	43.71	C
	16J	30	29	3.17	2.97	86.10	C

NOTES: [a] C = Contagious

R = Random

U = Uniform

as were the other tree species in these stands with the exception of lodgepole pine in Stand 20B. In Stands 1B, 2B, 10B and 13J, the total tree populations were also highly aggregated. However, in Stands 6J, 15J, 20B and 21W the total tree population was randomly distributed, indicating that the Presence of the other tree species tended to balance the contagion of the fir population. All eight stands had topographic irregularities, and the trees were visibly clumped.

Stand 8B was the only one in which the fir was regularly distributed; contagion of the associated pine population, however, was sufficient to make the total tree dispersion random. The uniform height and age of the fir population in this stand has already been shown (pp. 77 and 78).

No significant departure from random expectation was detected in Stands 5J, 7B, 9B, 11B, 17J and 18J. The only such departure in Stands 12J, 14J and 19B was found in the populations of pine and spruce, but this contagion did not affect the randomness of associated populations. However, in Stands 3J and 16J contagion of the spruce and pine populations was of such a scale as to produce a contagious total tree pattern, although the fir population was randomly distributed. Stand 4J resembled Stands 3J and 16J except that the density of tree species other than fir was negligible.

To summarize, the less abundant species such as

white spruce or lodgepole pine nearly always tend to be clumped within the dominant fir population. The distribution pattern of Douglas fir itself may be contagious or random but very rarely regular, and the inclusion of clumps of pine or spruce may or may not result in a change of pattern in the stand as a whole. The pattern of each stand should be assessed independently, and in conjunction with the complex of environmental and topographical factors peculiar to that stand.

Very high quadrat Frequencies coupled with low basal area and density values, indicated a uniform distribution for lodgepole pine in most stands. The variance-to-mean ratio, however, has indicated a contagious distribution. This discrepancy can be resolved by reference to the reproduction of pine. Lodgepole pine can only become established in canopy openings in a mature fir forest due to its low tolerance to shading. It can form dense, even-aged clumps in these openings which subsequently thin out with increasing intraspecific competition. More mature pine could be evenly distributed throughout the rest of the forest. This pattern of dense clumps of even-aged, young pine and widely scattered mature pine could explain this discrepancy in the results.

To provide further evidence for this hypothesis, four stands were chosen with a contagious distribution of pine as well as high Frequency and low density and basal area values for this species: Nos. 2B, 14J, 16J and 19B.

In each stand the mean DBH of pine in those quadrats with larger numbers of this species was considerably smaller than the mean DBH in those quadrats with a smaller number of pine. For example, the Frequency, density and basal area of pine in Stand 14J were 50%, 1.2 stems per 100 square meters and 7.5 square feet per acre respectively. In the six quadrats containing two trees or less the mean DBH was 7.3 inches, whereas in the four quadrats containing more than two trees the DBH was only 3.6 inches.

Random Point to Nearest Tree Distance Method (Pielou, 1959)

A second method of assessing the population dispersion of Douglas fir makes use of the distance measurements from random points (quadrat centers) to the nearest fir tree (see Chapter IV, page 58). It utilizes the relation between the mean of the measured distance, and the distance expected from the density obtained independently. The formula used (Pielou, 1959) is

$$\alpha = \pi D W$$

where $\pi = 3.14$, D = Density obtained independently (in trees per square foot), and W = Mean of the squares of the point-to-plant distances (in square feet).

A completely random distribution is indicated by the value of α equalling N-1/N, where N = number of distance

measures. A higher value of α is indicative of contagion and a lower value, of a regular distribution. The significance of departure from randomness is determined by the value of $2N\alpha$, which is distributed as Chi-square with 2N degrees of freedom.

The results showed that the Douglas fir population was clumped in Stands 4J, 6J, 10B, 12J and 21W. All other stands showed no significant departure from randomness (Table 15). These five stands were markedly different in topography, environment and population structure, and no explanation could be found for the pattern differences between these stands and the other 16.

A comparison of fir distribution pattern as depicted by the two methods showed poor agreement. For example, although Stands 6J, 10B and 21W were contagious according to both methods, Stands 4J and 12J showed no significant departure from random with the coefficient of dispersion method. Several stands showed the reverse trend of contagion with the coefficient of dispersion method but randomness with the distance measures method.

However, the latter method is independent of quadrat size, and is intended to detect non-randomness at any scale of pattern. Therefore it may only be sensitive to relatively large-scale departures from expectation, unlike the coefficient of dispersion method which is effective for detecting pattern only at the scale of the quadrat size used.

TABLE 15. WITHIN-STAND DISTRIBUTION PATTERNS OF DOUGLAS FIR POPULATIONS

Calculated from random point to nearest tree measurements (p. 58) at 5% significance level.

Stand	N[a]	Mean Distance (inches)	Density[b]	α[e]	$2N\alpha$[e]	d.f.[c]	Pattern[d]
1B	30	94.9	4.73	1.036	62.16	60	R
2B	30	115.6	3.33	1.104	66.24	60	R
3J	33	115.8	4.15	1.260	83.16	66	R
4J	20	120.1	4.45	1.778	71.12	40	C
5J	20	92.5	5.30	1.099	43.96	40	R
6J	22	91.7	9.45	2.316	101.90	44	C
7B	24	98.8	4.42	1.011	48.53	48	R
8B	20	99.1	4.10	0.948	37.92	40	R
9B	20	71.6	5.90	0.730	29.20	40	R
10B	25	135.1	4.20	2.378	118.90	50	C
11B	30	107.6	4.15	1.137	68.22	60	R
12J	20	98.9	7.50	1.657	66.28	40	C
13J	30	99.6	4.30	1.042	62.52	60	R
14J	20	98.1	4.80	1.154	46.16	40	R
15J	20	68.4	7.80	0.887	35.48	40	R
16J	30	139.3	2.47	1.099	65.94	60	R
17J	20	81.4	5.40	0.976	39.04	40	R
18J	22	117.2	3.59	1.195	52.58	44	R
19B	20	97.1	5.20	1.198	47.92	40	R
20B	20	85.4	6.60	1.337	53.48	40	R
21W	20	74.7	10.40	1.668	66.72	40	C

NOTES:
[a] N = Number of observations
[b] Density from quadrat counts in stems per 100 square meters
[c] d.f. = degrees of freedom
[d] C = Contagious; R = Random; U = Uniform
[e] See page 107.

An important objection to the coefficient of dispersion method, described previously, is that the proportion of a stand area suitable for the growth of trees is usually indefinite. Hence the appropriateness of the Poisson distribution cannot be determined and no conclusions made as to how closely the tree population approaches the carrying capacity of the habitat.

A significantly contagious distribution of a tree population should be readily observable on a subjective basis alone. In general, the results obtained from the coefficient of dispersion method gave better agreement with field observations. For example, the fir populations of Stands 4J and 12J were either random or regular by field observation, but certainly not clumped.

The distance measures method is most useful in forest vegetation where there are often practical difficulties in delimiting large quadrats necessary for sampling trees (Greig-Smith, 1964, p. 49). No problems of this nature were encountered in this study, so the point-to-tree distance measures lost some of their usefulness.

Shrub Stratum

1. Species composition

To compare the species composition of subordinate strata in different stands, it was desirable to have a single quantitative expression of population size for each species.

The prominence index used in calculating indices of similarity between stands (Chapter IX, page 186), and also in multiple regression analysis (Chapter VIII, page 162), was considered the best available value for this purpose. The prominence index combines cover and Frequency in the following formula:

$$(\sqrt{\text{Frequency}} \times \text{Cover}) + 1.0$$

The constant of 1.0 was added during the calculation of indices of similarity (Chapter IX, page 186) to give some weight to the Presence of a species in a stand irrespective of its cover and Frequency, and to lessen fluctuations in the prominence of rare species based on sampling error. This constant was retained in the prominence index as used for comparison purposes in this chapter and for dependent variables in multiple regression analysis in Chapter VIII, to keep the treatment of data consistent. For presentation purposes only, these indices were abbreviated to whole numbers and presented in the Presence list table (Table 16, pages 112 - 117). This prominence index has a range of 1 to 1001 units.

The mean total shrub cover was only 5.9%, and varied from 20.4% in Stand 21W to nil in Stand 5J. Only three other stands (Nos. 1B, 2B and 20B) had shrub cover exceeding 10% and these had very low tree canopy cover (Table 9, p. 94).

TABLE 16. PRESENCE LIST

Includes all species recorded in stands of Banff, Jasper and Waterton National Parks; listed quantitatively using basal area (trees) and prominence index (all other species, see page 111).

Species	Stands																				
	Banff									Jasper											Waterton
	1	2	7	8	9	10	11	19	20	3	4	5	6	12	13	14	15	16	17	18	21
Trees																					
Pseudotsuga menziesii	54	43	151	98	92	86	84	133	92	79	154	150	103	185	98	128	153	75	166	112	215
Pinus contorta	11	22	1	28	15	13	61	38	10	19	4	1	14	2	18	8	16	28	6	9	26
Picea glauca	1	2	1	3	2		6		1		1		15	51	1	5		7	2		
Populus tremuloides		1	2			2			2	1			2		1	1		2			1
Populus balsamifera						1															
Betula papyrifera														1							
Abies lasiocarpa																					1
Shrubs																					
Shepherdia canadensis	2	15	1	5	4	6	2	2	13	2	2	1	18	2	23	14	9	29	2	5	
Rosa acicularis	2	3	6	9	3	2	3	3	5	4	12	2	28	19	21	49	2	23	3	5	2
Spiraea lucida	1	12	2	3	2	3	9	3	21		2		2	1	7	14	2	12	2		46
Juniperus communis	38	129	1	2	29	7	2	15	47	1	1	1	2	4	1	1	2	6	6	1	
Symphoricarpos albus	7	2		1	2	2		2	2	2	5	1	17	3	1	1			1	2	14
Amelanchier alnifolia	5	3		1	2			2	7	1	2	1	1	2	7	2	1		1	2	2
Juniperus horizontalis	23	11	1	1	26	1	1	1	2				2								
Potentilla fruticosa	2	2						1	1				1								4
Ribes oxyacanthoides		2	1		1	3	1					1	1		1	1	1	1		2	2
Rosa woodsii	4	2			1				2		1		2		1				1	1	1
Elaeagnus commutata	1	1								1			1								
Salix spp. (2)[b]					1	1							2		1	2	1	1		1	1
Lonicera dioica													1	2	1	1					1
Symphoricarpos occidentalis																				1	
Rubus parviflorus																					90
Acer glabrum																					14
Rubus strigosus																					1
Cornus stolonifera																					1
Herbs and Dwarf Shrubs																					
Arctostaphylos uva-ursi	131	161	2	206	27	24	160	111	160	56	1		56	4	11	9	5	75	1	10	1
Elymus innovatus	23	11	185	45	9	90	94	50	30	126	146	139	94	119	93	141	34	152	100	69	
Fragaria virginiana	2	2	5	2	2	13	27	17	4	6	7	2	8	2	15	6	1	5	10	8	9
Aster conspicuus	2	2	31	2	4	9	2	2	2		4	2	20	6	1	32		10	6	3	63
Galium boreale	3	3	3	2	4	2	2	2	2	2	5	2	2	2	1	2		2	2	2	2
Achillea millefolium	2	2	2	2	4	5	2	1	2	2	2	1	1		2	2	1	2	2	2	

TABLE 16. (continued)

Species	Stands: Banff 1	2	7	8	9	10	11	19	20	Jasper 3	4	5	6	12	13	14	15	16	17	18	Waterton 21
Linnaea borealis		1		28			41	2	2	2	1		13	52	16	12	15	45	1	1	
Solidago decumbens	2	2	2	5	6	1	2	2	16	2	3	1	2	1	2		1	2	1	5	1
Campanula rotundifolia	1	1	1	1	1	2		1	1	1	1	2	1		1	1	1	1	1	2	2
Lathyrus ochroleucus			3	5	2	3	5	2	1		1	1	2		2	17		3	2	1	
Vicia americana			4	1	2	2	5	1	1		2	1	1		2	3			8	1	
Koeleria cristata	40		1		2	1			1	6	1	1	1				1	1	1	4	
Festuca saximontana	1	1			1	2	1		1	2	1	2			2		1	1	1	2	
Anemone multifida	1	2		2	2	2	2	1	1	2	2	1	1					1	1	1	1
Viola adunca	2	2	1	2	2	2	1	1	2	2	1	1			1	2			1	1	
Astragalus decumbens	11	2	7	14	7	34	21	10	13	18	3	1						1	7	2	
Allium cernuum	2	2	2		2	5	1	1	1	1	1	1						1	2	1	1
Castilleja miniata	1	1	1	1		1	1	1	1				1		1	1		1			1
Aster laevis var. *geyeri*	2	3		1	7	1	1	2	2									1		1	1
Senecio canus	3	2	1	1	1	1	2		1		1										
Hedysarum sulphurescens	2	2	2	7	1	1	24	10	4												1
Calamagrostis rubescens			80	92	29	186	153	91	57												1
Agoseris glauca	1		1	2	1	2	3														
Carex concinnoides		1		35		2	21														
Comandra pallida	2	1			1				1												
Festuca scabrella	3		1	5			8	6	2	1											
Penstemon confertus	2	2	1		1	2													1		
Sedum stenopetalum	1		2	1		1	1												1		
Linum lewisii	1	1			1				1				1								
Oxytropis campestris		1	1			2	3	1	1	2			1								
Zygadenus elegans	2		1	1		1	2	1						1				1			
Astragalus striatus	1		1		1				1	1		1									
Anemone patens	2	2	1		1						1		1								
Gaillardia aristata	2	2			1				1	2	1		1								
Antennaria rosea	2				1	6	2			1						1					
Artemisia frigida	2				1	1			1				1							1	
Stipa columbiana	1				4	2			2							1			2	1	
Antennaria neglecta		1		2			2	4	1	2					1	1			1		
Arnica cordifolia			1	1		2	1	1			1		1		1	1		10	1		7
Carex umbellata			1		2	1	1		2	3	2	1	2			1				1	
Agropyron dasystachyum	2		1	2		2				5	5	3	5						1	5	
Antennaria nitida				2	1			2	1			1			1		1		1	1	
Taraxacum sp.	2	1	1		1	5	1			1	1	1							2		
Disporum trachycarpum		1	1					1			1			4	1	1		1			7
Androsace septentrionalis	1	1	1							1	1	1							1		
Bromus pumpellianus		5						2	1	1		1	1					1			
Hieracium canadense	1	2						2							1	1			1	1	
Poa spp. (4)[b]	22	39	5		1	2		1	1	6	4	12	1		1	1	1	2	3	2	
Senecio cymbalarioies										2	1	1	1		1	1	1		1	2	
Gentianella amarella	1							1		1	1	1			2	1		2	2	1	

TABLE 16. (continued)

Species	Stands																				
	Banff									Jasper											Waterton
	1	2	7	8	9	10	11	19	20	3	4	5	6	12	13	14	15	16	17	18	21
Epilobium angustifolium	1					1						1	1		1	1	1	2	1		
Pyrola secunda			1				2							2	2	1	1	2			5
Pyrola virens		1		1				1		1	1			1	1	1	2	1			2
Clematis verticellaris			1			1						1		1	1	1		1			8
Oxytropis splendens				1		2				2	1	1	1							1	
Arabis holboellii	1				1	2			1	1		1			1	1		1	2	1	
Stellaria longipes						1					1							1	1	1	
Potentilla sp.											2										
Calypso bulbosa	1		1							1	1						1	2			
Aster sibiricus		1								1			1				1				
Goodyera repens																2	1		1		
Geocaulon lividum														12	1			1			
Saxifraga bronchialis																	1		1	1	
Antennaria racemosa											1							3	1		
Geum triflorum										1	1										
Arenaria lateriflora											1	1									
Aster ciliolatus													1	2							
Viola rugulosa														2		4					2
Cornus canadensis															1	1					
Potentilla pensylvanica																			1	1	
Thalictrum occidentale (?)																1					56
Hieracium albiflorum																			1		1
Kobresia simpliciuscula										1											
Corallorhiza trifida													1								
Phleum pratense													1								
Lilium philadelphicum														1							
Apocynum androsaemifolium															1						
Crepis atrabarba															1						
Actaea rubra																1					1
Vaccinium caespitosum																1					1
Galium triflorum																1					1
Viburnum trilobum																1					
Osmorhiza depauperata																1					
Ribes glandulosum																	1				
Hedysarum alpinum																		2			
Saxifraga tricuspidata																		1			
Agropyron subsecundum																				1	
Chenopodium album																				1	
Chenopodium capitatum																				1	
Erigeron compositus		1				7				1									1	1	
Oxytropis deflexa						5					1								1		
Cystopteris fragilis													1				1			1	1
Selaginella densa						1											1		1		
Carex richardsonii								35	12	1								4			

TABLE 16. (continued)

Species	Stands																					
	Banff									Jasper												Waterton
	1	2	7	8	9	10	11	19	20	3	4	5	6	12	13	14	15	16	17	18	21
Carex concinna	7	10								1				6								
Erigeron glabellus	1						1			2			1									
Arabis hirsuta	1	1									1								1			
Habenaria viridis			1	1				1					1						1			
Cerastium arvense	1		1			1				1												
Aster alpinus			1							1												
Trisetum spicatum						1													1			
Calamagrostis purpurascens	1																1					
Hedysarum mackenzii	2	1																				
Oxytropis sericea	1				1																	
Agropyron spicatum	1							1														
Erigeron caespitosus	3								1													
Chrysopsis villosa	1								1													
Chrysanthemum leucanthemum	1																					
Orthocarpus luteus	1																					
Erysimum inconspicuum	1																					
Sisyrinchium montanum	1																					
Agropyron griffithsii			1		4																	
Lomatium simplex			1		1																	
Collinsia parviflora			1			1																
Osmorhiza chilensis			1																			8
Dodecatheon conjugens			1																			
Stenanthium occidentale			1																			
Danthonia intermedia			1																			
Stipa richardsonii		1							1													
Artemesia campestris					1				1													
Zygadenus gramineus					1																	
Draba aurea (?)						1																
Smilacina racemosa						1																13
Heuchera cylindrica						1																1
Elymus glaucus																						1
Bromus vulgaris																						2
Festuca occidentalis																						5
Carex geyeri																						15
Clintonia uniflora																						6
Veratrum eschscholtzii																						1
Xerophyllum tenax																						1
Goodyera oblongifolia																						6
Mahonia repens																						36
Chimaphila umbellata																						1
Monarda fistulosa																						1
Aquilegia brevistyla (?)																						1
Balsamorhiza sagittata																						1

TABLE 16. (continued)

Species	Stands: Banff 1	2	7	8	9	10	11	19	20	Jasper 3	4	5	6	12	13	14	15	16	17	18	Waterton 21
Senecio pseudaureus (?)																					1
Polypodium vulgare																					1
Bryophytes																					
Abietinella abietina	2	1	1	1	1	1	8	7	1	6	1	1	28	103			6	1		1	
Hypnum revolutum[a]																					
Drepanocladus uncinatus[a]	7	1	1	19	1	2	22	68	2	1			7	1	1	1	10	7	3	1	2
Hylocomium splendens		1	1	2		2	63	11	1	13	16	7		506	12	55	236	45	19	1	
Tortula ruralis		1	5		4	10	2	2		5	11	1	16	2	6	1	6	3	2	3	1
Polytrichum juniperinum				1		1				1				1	1	2	1	1	2		
Dicranum rugosum				1			1				1	1			4	1	2	3	1	1	2
Pleurozium schreberi		1					4								12	16	3	9	1		
Ptilium crista-castrensis	1	1											3		1	1			2	1	
Orthotrichum macounii						1						1			1		2	1	1	7	
Dicranum fuscescens								1			1					1	1	2	1		
Rhytidium rugosum										2	1	1		1			29			2	
Hedwigia ciliata																	4		1	1	
Ptilidium ciliare																1		1		1	
Ceratodon purpureus									1	1		1				4	2				
Pohlia nutans							6			1		1		2					2		
Brachythecium salebrosum							1		1	1					5			1			2
Ditrichum flexicaule								1		1				1							
Barbilophozia hatcheri							1								1			1			
Eurhynchium pulchellum			1												1						
Rhytidiadelphus triquetrus														1							
Tortella tortuosa														1							1
Timmia austriaca																		1			
Schistidium alpicola												1									
Dicranum fragilifolium																1					
Pylaisia polyantha									1												
Ptilidium pulcherrimum																1					
Lophocolea minor																1					
Mnium lycopodioides[a]																					
Mnium spinulosum[a]																					2
Lescuraea radicosa																					6
Camptothecium aureum																					1
Dicranum scoparium																					2
Lichens																					
Peltigera spp. (5) below[a]	11	2	2	64	2	11	106	50	6	14	18	6	6	17	54	57	29	77	12	3	1
Peltigera canina var. *rufescens*	X[c]	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Peltigera canina					X				X							X					

TABLE 16. (continued)

Species	Stands																			
	Banff									Jasper										Waterton
	1	2	7	8	9	10	11	19	20	3	4	5	6	12	13	14	15	16	17	18	21
Peltigera aphthosa						X									X	X	X	X	X	X	
Peltigera aphthosa var. *variolosa*			X	X		X					X			X							
Peltigera horizontalis or *P. polydactyla*			X	X	X		X	X		X				X				X			
Cladonia spp.[b]	6	2		6		4	9	2	1	4	1	1		2	55	11	19	15	9	22	2
Parmelia spp. (4) below[a]		2	3	2	1	2			1		1			1	4	2	5	1	2	2	2
Parmelia sulcata		X	X			X			X		X				X	X	X		X	X	X
Parmelia physodes		X	X	X										X	X		X	X			
Parmelia enteromorpha																					X
Parmelia conspersa																				X	
Usnea spp.[b]		1	2			3			1						1	1	2		2		1
Letharia vulpina			2			2			1						1	1	2		2		1
Cetraria nivalis	1			1				1		2	1						1	2		2	
Cetraria islandica							1	1							1		1	1		1	
Stereocaulon tomentosum							1				1				1		1	1		1	
Lobaria pulmonaria															1		3				
Cetraria cucullata												1								1	
Cetraria glauca															1						1
Cetraria pinastri									1								1				
Physcia sp.	1																				
Leptogium saturninum																				1	

NOTES: [a] Sampling confusion between species resulted in a combined Prominence Index

[b] Number of species (unnamed) included in a combined Prominence Index

[c] X denotes 'present'.

Plate 3 Stand 11, July 1965; an interior view of a vigorous, young-medium aged stand of Douglas fir with lodgepole pine and white spruce. The understory vegetation is predominantly *Elymus innovatus*, *Calamagrostis rubescens* and *Arctostaphylos uva-ursi* in a well-developed herb and dwarf shrub stratum. The shrub stratum is very sparse.

Plate 4 Stand 17, August 1965; a dense, medium-aged Douglas fir stand with a very sparse understory composed predominantly of *Elymus innovatus*.

Only seven shrub species had mean prominence indices of over 1; these were, in order of decreasing prominence: *Juniperus communis* (14), *Rosa acicularis* (10), *Shepherdia canadensis* (7), *Spiraea lucida* (7), *Juniperus horizontalis* (3), *Symphoricarpos albus* (3) and *Amelanchier alnifolia* (2).

In Banff and Jasper, *Juniperus communis*, *Rosa acicularis* and *Shepherdia canadensis* provided the majority of the shrub cover, but only *Juniperus* had individual stand values in excess of 5% (in Stands 1B, 2B and 20B). However, six of the seven most prominent species had mean quadrat Frequencies in excess of 10%. *Rosa*, *Shepherdia* and *Spiraea* Frequencies were extremely high, with mean values of 62%, 45% and 45% respectively (Table 10, p. 95). *Shepherdia* was absent only from Stand 21W and *Spiraea* from Stands 3J, 5J and 18J.

Juniperus communis had a relatively low Frequency in most stands and was generally limited to canopy openings but provided dense cover in these areas. *Rosa*, *Shepherdia* and to a lesser extent *Spiraea* had little cover, but high Frequency indicative of a uniform, within-stand distribution pattern, less critically dependent on light intensity and other environmental differences associated with openings.

Amelanchier alnifolia, *Symphoricarpos albus* and *Juniperus horizontalis* were occasionally high in Frequency but consistently low in cover values.

Populations of other shrub species were usually of

negligible size. *Potentilla fruticosa* and *Rosa woodsii* were prominent in those stands with low tree canopy cover, and tended to be associated with *Juniperus communis* and *J. horizontalis* in openings. *Salix* species were also very restricted in occurrence. It was suspected from vegetative characteristics, that all specimens were either *S. bebbiana* Sarg. or *S. scouleriana* Barratt.

Stand 21W at Waterton was atypical in that high shrub cover was paralleled by a high total tree cover. The higher carrying capacity of this stand, very apparent from data on basal area, tree cover, herb cover etc., indicated that other factors as well as light intensity are operative in determining the total shrub cover. More than half of the shrub cover of 20.4% in Stand 21W was provided by *Rubus parviflorus*, a species not found in Banff or Jasper stands. This stand had a very different species composition to the Banff and Jasper areas: principal species with their prominence indices were *Rubus parviflorus* (90), *Spiraea lucida* (46), *Acer glabrum* (14) and *Symphoricarpos albus* (14). All had very high Frequencies but only *Rubus* had cover exceeding 5% (12.0%). The latter species provided almost continuous cover over the more open parts of the stand at a height of about 2½ feet.

2. Density

The different growth habits of the major shrub species made comparisons of their density of doubtful use

(Table 17). *Spiraea lucida*, *Rosa acicularis*, *Amelanchier alnifolia* and *Symphoricarpos albus* usually grew as evenly-distributed single stems, and therefore had disproportionately high stem densities. *Shepherdia canadensis*, *Juniperus communis* and *J. horizontalis* usually grew as small numbers of dense bushes, each with several large stems.

3. Height

Shrubs of most species varied but little about a mean height between and within stands (Table 18). The mean height of the shrub stratum was completely dependent on the species composition; sudden changes of environment tended to result in changes in composition rather than height changes in the same species.

Spiraea, *Amelanchier* and *Symphoricarpos* were rarely more than 1 foot tall, and usually varied between 6 inches and 1 foot. Field observations indicated that many individuals had been browsed down to this height repeatedly, probably by elk or mule deer. It is possible that the browse level was determined by snow depth in winter, because Douglas fir forests in Banff and Jasper could be important winter feeding grounds for these ungulates. In Stands 13J and 21W, *Amelanchier* was 3 to 4 feet tall in places, suggesting that browsing activity was comparatively light. It is therefore probable that the low height of these shrubs is limited more by browsing than by poor habitats.

TABLE 17. DENSITY ESTIMATES FOR SPECIES OF THE SHRUB STRATUM

Expressed as stems per 16 square meters and includes only those species with a presence value greater than 20%.

Species	Stands																				
	Banff									Jasper											Waterton
	1	2	7	8	9	10	11	19	20	3	4	5	6	12	13	14	15	16	17	18	21
Rosa acicularis	1.6	4.7	5.9	16.3	3.5	3.5	3.5	13.4	8.3	6.2	6.3	0.5	13.6	8.9	19.7	22.8	1.3	7.5	2.6	2.3	0.7
Shepherdia canadensis	11.6	11.9	0.2	4.7	2.0	2.8	3.8	2.1	7.3	4.1	1.8	0.3	6.9	1.4	5.8	9.6	4.0	25.5	1.3	5.0	
Spiraea lucida		6.9	2.0	3.6	9.3	11.4	9.5	13.1	12.8		0.6		2.6		5.1	7.5	0.6	7.9	3.1		23.3
Juniperus communis	13.2	23.7	0.8	2.6	7.5	1.8	1.6	4.3	6.2	0.5			0.7	0.8			0.9	2.1	1.8	0.1	
Symphoricarpos albus	4.0	0.6		0.1	2.0	0.2		0.9	1.6	2.2	5.4		10.1	6.2		0.2				0.9	4.6
Amelanchier alnifolia	5.4	0.9			0.3			0.7	5.9	0.1	0.2			0.2	5.3	0.7				0.6	1.3
Juniperus horizontalis	9.4	2.8	0.1		4.1	0.1			0.6				0.4								
Rosa woodsii	2.9	2.2							0.6				1.7								
Ribes oxyacanthoides		0.3	0.1			2.6									0.3			0.3		0.3	0.8
Potentilla fruticosa	13.8	1.2							0.4												

TABLE 18. HEIGHT ESTIMATES FOR SPECIES OF THE SHRUB STRATUM

Expressed as the average maximum[a] height in feet.

Species	Stand: Banff 1	2	7	8	9	10	11	19	20	Jasper 3	4	5	6	12	13	14	15	16	17	18	Waterton 21	Mean in inches
Shepherdia canadensis	2	2	½	1½	2	2½	2	1½	3½	2	1½	2	4[b]	2	2[c]	4½	2½	4	4	2½		29
Rosa aciclularis	½	½	½	½	1	2	1	½	½	½	½	½	2[b]	1	1[c]	2½	½	1	1	1	2	13
Spiraea lucida		½	½	½	½	½	1	½	½		½		1	½	½	½	½	1	½		1½	8
Juniperus communis	1½	1½	1½	1½	1½	1½	1½	1½	1½	1½	1	1½	½	1	1½	1½	½	1½	1	1		16
Symphoricarpos albus	½	½		½	½	½		½	½	½	½	½	1	½	½	½			1½	½	1½	8
Amelanchier alnifolia	½	½		½	½			½	½	½	½	½		½	1[c]	1	½		1	1	3	10
Juniperus horizontalis	1	1	½	1	1	1		1	1				½									11
Potentilla fruticosa	1½							1	1				1½								1	14
Ribes oxyacanthoides		1	1½		½	2						½			1½		1	1		1½	1½	15
Rosa woodsii		½			½				½		½		1		1				1½	1	2½	14
Elaeagnus commutata	2	1½								1			1½									18
Salix spp. (3)					3								1½		6	4	3	2		2	1½	34
Lonicera dioica														½	½						½	8

NOTES: [a] 'Average Maximum': the average height of the mature shrubs. [b] Occasional plants up to 6 feet in height in S.E. corner of stand. [c] Occasional plants up to 4 feet in height at bottom of slope. [d] In stand 21: *Acer glabrum* 5, *Rubus parviflorus* 2½, *Cornus stolonifera* 3 feet in height.

Rosa acicularis and *R. woodsii* varied between 6 inches and 2½ feet in height, and browsing did not seem as common in populations of *Rosa* as in those of the preceding three species.

Juniperus communis and *J. horizontalis* appeared to be little subject to browsing activity, and were very consistent in height, reaching maxima of 1½ feet and 1 foot respectively. Even under more favourable environmental conditions these heights were rarely exceeded.

With the exception of occasional *Salix* species, *Shepherdia canadensis* was the tallest shrub. It varied considerably in height from stand to stand, ranging from 1½ to 6 feet and averaging about 2½ feet. There was very little evidence of browse on this shrub and it is possible that the taller height of *Shepherdia* results from preferential consumption of other associated shrubs.

To summarize, many stands had a shrub stratum composed of two layers: one of *Shepherdia canadensis* averaging about 2½ feet in height; the second composed of the remaining shrub species, with the exception of *Salix*, and varying from 6 to 18 inches in height.

Herb and Dwarf Shrub Stratum

The mean total cover of herb and dwarf shrub species was only 30.2% (Table 20); this figure somewhat exceeds actual stratum cover because more than one species

TABLE 19. QUADRAT FREQUENCY PERCENTAGES FOR SPECIES OF THE HERB AND DWARF SHRUB STRATUM AND BRYOPHYTE AND LICHEN STRATUM

Includes only those species with both a mean frequency of 10% or over and a presence value of 20% or over; and using 1x1 meter quadrats.

	Stands																					
	Banff									Jasper											Waterton	
Species	1	2	7	8	9	10	11	19	20	3	4	5	6	12	13	14	15	16	17	18	21	Mean
Herbs and Dwarf Shrubs																						
Elymus innovatus	23	23	92	95	20	76	90	90	70	94	100	100	95	100	90	100	75	100	70	82		79
Arctostaphylos uva-ursi	73	87	4	100	65	24	90	65	70	57	5		65	10	27	25	5	57		23		43
Fragaria virginiana	7	37	25	30	20	56	85	85	30	36	50	15	55	25	67	35		17	25	27	40	36
Aster conspicuus	7	37	83	20	25	40	15	10	30		45	40	55	20		60		27	30	18	60	28
Calamagrostis rubescens			46	75	45	76	85	90	75												5	25
Astragalus decumbens	43	37	25	40	35	44	40	25	35	48	15								10	18		21
Linnaea borealis				35			60	5	5	3			35	85	37	30	40	70		4		20
Solidago decumbens	17	27		50	45		15	50	60	24	15		10		10		5	10		27		18
Galium boreale	33	33	29	25	40	36	15	15	10	21	20	10	20	15		10		10	5	14	20	18
Achillea millefolium	27	13	12	15	25	44	10	5	10	33	25				17	10		7	10	27	5	15
Hedysarum sulphurescens	13	23	21	65			65	60	40													14

TABLE 19. (continued)

Species	Stands																						
	Banff									Jasper											Waterton	Mean
	1	2	7	8	9	10	11	19	20	3	4	5	6	12	13	14	15	16	17	18	21	
Bryophytes and Lichens																						
Peltigera spp.	33	3	12	80	10	40	95	80	15	42	45	15	35	75	73	55	75	83	40	59	5	48
Cladonia spp.	20	10		20		28	40	30		24	5	10		10	70	40	65	57	30	50	15	25
Hylocomium splendens				10		8	50	25		12	30	10		95	27	45	85	37	25	4		23
Tortula ruralis			12	5	15	44	15	10		12	20		30	10	33	5	35	27	15	14	5	15

TABLE 20. PERCENTAGE COVER OF THE HERB AND DWARF SHRUB STRATUM AND THE BRYOPHYTE AND LICHEN STRATUM AND THEIR MAJOR SPECIES

Includes only those species with both a mean cover of 0.5% or over, and a presence of 20% or over.

	Stands																					
	Banff									Jasper											Waterton	
Species	1	2	7	8	9	10	11	19	20	3	4	5	6	12	13	14	15	16	17	18	21	Mean
Herbs and Dwarf Shrubs																						
Elymus innovatus	4.5	2.2	19.2	4.5	1.8	10.2	9.8	5.2	3.5	12.9	14.5	13.8	9.5	11.8	9.7	14.0	3.8	15.2	11.8	7.5		9.3
Arctostaphylos uva-ursi	15.2	17.2	0.6	20.5	3.2	4.6	16.8	13.7	19.0	7.3			6.8	1.0	2.0	1.5	0.8	9.8		1.8		7.1
Calamagrostis rubescens			11.7	10.5	4.2	21.2	16.5	9.5	6.5												0.2	4.0
Linnaea borealis				4.5			5.2	0.5	0.5	0.5			2.0	5.5	2.5	2.0	2.2	5.3				1.5
Astragalus decumbens	1.5		1.2	2.0	1.0	5.0	3.2	1.7	2.0	2.4	0.5	0.2							1.8	0.2		1.1
Fragaria virginiana	0.2		0.8	0.2		1.6	2.8	1.7	0.5	0.8	0.8	0.2	1.0	0.2	1.7	0.8		1.0	1.8	1.4	1.2	0.9
Aster conspicuus			3.3		0.5	1.2			0.2		0.5	0.2	2.5	1.2	0.2	4.0		1.7	1.0	0.5	8.0	0.9
Total Herb and Dwarf Shrub spp.	36.9	28.8	41.0	48.6	15.7	51.2	65.3	40.0	38.0	29.3	20.1	17.9	23.0	22.7	17.2	27.0	7.5	36.7	20.0	14.1	32.6	30.2
Bryophytes and Lichens																						
Hylocomium splendens				0.2			8.8	2.0		3.5	2.8	1.8		51.8	2.2	8.0	25.5	7.2	3.5			5.9
Abietinella abietina	0.5						1.2	1.5		2.7			4.2	11.8			1.0	0.2				1.2
Peltigera spp.	1.8	0.3	0.4	7.0		1.6	10.8	5.5	1.2	2.0	2.5	1.2	2.5	1.8	6.2	7.5	3.2	8.3	1.8	0.2		3.3
Cladonia spp.	1.0	0.3		1.0		0.6	1.2	0.2		0.6	0.2			0.2	6.4	1.5	2.2	1.8	1.5	3.0		1.1
Total Bryophyte Cover	2.0		1.2	3.7	0.8	2.0	16.7	11.9	0.4	7.8	5.0	1.8	9.0	64.3	9.2	12.7	36.0	12.2	6.4	1.8	1.4	9.8
Total Lichen Cover	2.8	0.6	0.8	8.0		2.6	12.2	5.7	1.2	2.8	2.7	1.2	2.5	2.0	13.3	9.2	6.6	10.3	3.5	3.4		4.6

occasionally covered the same sampling point. Seven herb and dwarf shrub species had mean prominence indices of significant magnitude: *Elymus innovatus* (83), *Arctostaphylos uva-ursi* (58), *Calamagrostis rubescens* (33), *Linnaea borealis* (11), *Aster conspicuus* (10), *Fragaria virginiana* (7) and *Astragalus decumbens* (7) (Table 16, pp. 112 - 117).

Elymus and *Arctostaphylos* were responsible for well over half of the total cover at Jasper, and together with *Calamagrostis* accounted for a similarly large fraction at Banff. These three species alone accounted for 20.4% out of the total cover of 30.2% (Table 20).

Fragaria and *Aster conspicuus*, like *Elymus* and *Arctostaphylos*, were present in nearly all of the stands and had high Frequencies within them (Table 19). Their mean cover values were less than 1%, however.

The populations of *Linnaea* and *Astragalus decumbens* were less widely distributed among stands than those of the other five prominent species with the exception of *Calamagrostis*. Prominence indices of *Linnaea* and *Astragalus* varied greatly from stand to stand with those of *Linnaea* ranging from zero to 52 in Stand 12J, and those of *Astragalus* from zero to 34 in Stand 10B. Both *Astragalus* and *Calamagrostis* were mainly restricted to Banff.

The remaining 134 species present in this stratum were of only minor importance, and contributed little to the cover, although the following had mean Frequencies of over 10%: *Solidago decumbens*, *Galium boreale*, *Achillea*

millefolium and *Hedysarum sulphurescens* (Table 19). Many of these generally insignificant herbs and dwarf shrubs had high prominence indices in one or a few stands. These larger populations were in many cases associated with atypical environmental conditions or marked variance in the cover of the tree canopy. For example, in Stand 12J the following species were quite prominent, and seemed to be associated with a high proportion of white spruce in the canopy, and a continuous carpet of bryophytes: *Geocaulon lividum*, *Carex concinna*, *Pyrola secunda* and *Disporum trachycarpum*. Exceptionally high prominence indices were recorded for *Koeleria cristata* (40) in Stand 1B, species of *Poa* (39) in Stand 2B, *Carex concinnoides* (35) in Stand 8B, *Hedysarum sulphurescens* (24) in Stand 11B and *Carex richardsonii* (35) in Stand 19B.

A group of "differential species" (Damman, 1964, p. 7) is apparent for the Banff stands. The major species of this group is *Calamagrostis rubescens*; others include *Hedysarum sulphurescens*, *Senecio canus*, *Agoseris glauca*, *Festuca scabrella* and *Penstemon confertus*. Many other species were more common at Banff than at Jasper, including *Arctostaphylos uva-ursi*, *Astragalus decumbens*, *Solidago decumbens* and *Aster laevis*.

However, no such group of differential species is apparent for the Jasper stands, and only *Elymus innovatus* and *Linnaea borealis* of the more prominent species were more common in this region than at Banff. It is possible that

this phenomenon results in part from the greater number of open spaces, and corresponding habitat diversity, in some of the Banff stands.

A large number of the herbs with low Presence values and prominence indices were considered to be "unsuccessful adventives" (Braun-Blanquet, 1932, p. 46), as they were far more abundant in other ecosystems nearby. For example, a number of grassland species from a nearby meadow infiltrated Stand 7B and were included in its Presence list: *Dodecatheon conjugens*, *Danthonia intermedia*, *Agropyron griffithsii*, *Lomatium simplex*, *Penstemon confertus* and *Senecio canus*. Stand 12J graded into a white spruce forest and consequently included a number of species more typical of that ecosystem: *Linnaea borealis*, *Pyrola secunda*, *Pyrola virens* and *Geocaulon lividum*.

The herb and dwarf shrub flora in Stand 21W at Waterton was very different from those of stands in Banff and Jasper. The following had prominence indices of 10 or over in Stand 21W, but were absent or rare in the other 20: *Thalictrum occidentale*, *Mahonia repens*, *Carex geyeri*, *Smilacina racemosa* var. *amplexicaulis*, *Osmorhiza chilensis*, *Clintonia uniflora*, *Goodyera oblongifolia* and *Festuca occidentalis*. Ten other species were found only in Stand 21W but these were of only minor quantitative significance.

Terrestrial Bryophyte and Lichen Stratum

Bryophytes

The mean total bryophyte cover for all stands was 9.8%, and varied from a maximum of 64.3% in Stand 12J to zero in Stand 2B (Table 20). This wide fluctuation was principally caused by *Hylocomium splendens*, which accounted for 5.9% out of the total mean cover of 9.8%. *Hylocomium* was the only species with a high mean prominence index (47), and was especially prominent in Stand 12J (506), Stand 15J (236), Stand 11B (63), Stand 14J (55) and Stand 16J (45) (Table 16, pp. 112 - 117). These five stands appeared to have little in common to account for this abundant *Hylocomium* carpet. The largest value, in Stand 12J, was undoubtedly connected with an atypically large proportion of white spruce in the canopy; but the canopy of Stand 11B, with the second largest index, had a large proportion of lodgepole pine instead. The other three stands have little spruce or pine in their canopies. Few similarities in total tree cover (Table 9, p. 94), basal area (Table 8, p. 92), shrub cover (Table 9, p. 94), topography (Appendix 1, p. 266), soil (Table 21), etc., were found.

Hylocomium was absent or rare on dry, exposed, south-facing slopes (Stands 1B, 2B, 7B, 9B and 20B), and where shrubs and herbs formed a dense undercover (Stands 6J and 21W).

The other bryophytes with noteworthy mean

TABLE 21. PHYSICAL AND CHEMICAL PROPERTIES OF THE SOILS

Stand	Horizon in inches	Texture Class[c]	Percentages in 0-2 mm Fraction				Conductivity mmhos.	Free Lime	pH	Available Nutrients lbs per acre			% Gravel (over 2 mm)	Dominant Rock Type[d]
			Sand	Silt	Clay	Water Availability				Ne	Pe	Ke		
1B	¼-1	Humus					0.7	Low	7.4	11	20	568		
1B	1-5	SCL	53	21	26	7.4	0.5	Med	7.9	2	4	282	28	Q,L
1B	5-5½	L	49	30	21	18.6	0.7	High	7.9	1	1	140	12	L,Q
1B	5½-18+[b]	SCL	52	26	22	14.6	0.6	V. High	8.0	2	1	104	25	Q,L,SH
2B	½-2	Humus					0.6	High	8.0	1	1	508		
2B	2-8	L	50	34	16	14.0	0.5	V. High	7.9	1	0	60	41	L,Q
2B	8-18+	L	47	34	19	15.5	0.6	High	7.9	1	0	42	63	L,Q
3J	½-2	Humus					0.6	Nil	7.1	2	20	248		
3J	2-6	SL	56	33	11	17.1	0.5	Nil	7.5	1	12	146	15	QC
3J	6-18+	SL	62	26	12	13.2	0.5	Nil	7.5	1	7	124	45	QC
4J	¼-1	Humus					0.6	Nil	6.9	2	44	444		
4J	1-3	L	44	38	18	16.3	0.4	Nil	6.7	2	39	536	3	
4J	3-7	L	49	30	21	9.7	0.3	Nil	6.5	1	9	146	8	QC
4J	7-18+	L	40	34	26	11.1	0.4	Nil	6.9	1	9	114	40	QC
5J	¼-1	Humus					0.4	Nil	6.8	0	35	308		
5J	1-4	L	49	33	18	13.1	0.3	Nil	6.5	0	30	290	4	QC
5J	4-15	SL	55	25	20	10.4	0.2	Nil	6.4	1	6	104	27	QC
6J	½-2	Humus					0.7	V. Low	7.4	1	46	220		
6J	2-15	L	37	45	18	14.1	0.5	Low	8.0	2	19	260	1	
6J	15-24+	L	38	38	24	10.4	0.5	Med	8.0	1	23	308	51	QS,L
7B	½-2	Humus					0.6	Nil	7.4	22	14	324		
7B	2-8	L	46	35	19	12.4	0.6	High	7.9	18	6	116	42	L
7B	8-15	L	39	36	25	9.1	0.5	V. High	8.0	3	1	88	56	L
8B	¼-1	Humus					0.6	Nil	7.0	1	16	252		
8B	1-5	L	49	34	17	7.8	0.6	Nil	7.0	0	9	228	18	L
8B	5-7	L	46	28	26	11.2	0.6	High	7.8	1	13	238	32	L,Q
8B	7-21+	CL	39	31	30	10.1	0.6	V. High	8.1	1	0	62	33	L
9B	¼-1½	Humus					0.6	V. Low	8.0	2	4	566		
9B	1½-5	SL	54	36	10	13.4	0.6	High	8.0	1	0	230	46	L,Q
9B	5-11	SL	56	34	10	14.6	0.6	High	8.1	3	1	88	26	L
9B	11-24+	SL	66	26	8	8.9	0.7	High	8.1	5	0	52	44	L,Q
10B	½-2	Humus					0.5	Nil	6.8	2	25	286		
10B	2-10	L	39	40	21	23.3	0.6	Nil	7.2	2	67	140	46	SH
11B	½-1	Humus					0.6	Nil	6.6	1	23	304		
11B	1-8	L	42	43	15	16.6	0.5	Nil	6.5	2	8	288	1	
11B	8-15+	SL	62	24	14	6.7	0.6	High	7.7	1	9	120	57	L,Q
12J	½-1	Humus[a]												
12J	1-4	StL	20	56	24	22.9	0.5	Nil	7.0	3	4	416	0	
12J	4-15+	L	44	37	18	16.9	0.6	High	7.9	3	2	200	6	L
13J	½-1½	Humus					0.5	Nil	7.2	1	25	600		
13J	1½-8½	SL	61	26	13	9.7	0.4	Nil	7.1	3	20	294	38	SL,QC
13J	8½-15+	SL	63	22	14	8.5	0.4	Nil	6.1	1	8	78	45	SL,QC

TABLE 21. (continued)

Stand	Horizon in inches	Texture Class[c]	Percentages in 0-2 mm Fraction				Conductivity mmhos.	Free Lime	pH	Available Nutrients lbs per acre			% Gravel (over 2 mm)	Dominant Rock Type[d]
			Sand	Silt	Clay	Water Availability				N[e]	P[e]	K[e]		
14J	½-2	Humus					0.3	Nil	6.5	3	28	342		
14J	2-8	SL	55	33	12	12.9	0.4	Nil	6.9	5	41	460	6	SL,QC
14J	8-14	SL	67	17	16	7.4	0.5	Nil	6.9	1	8	98	58	SL,QC
15J	½-1	Humus					0.5	Nil	6.8	1	20	408		
15J	1-2½	SL	60	30	10	14.1	0.4	Nil	7.2	1	16	308	6	
15J	2½-10	SL	65	23	12	10.9	0.3	Nil	6.0	1	32	160	6	
15J	10-18+	LS	83	9	8	3.4	0.2	Nil	6.4	3	9	62	25	QC,QS
16J	½-2¼	Humus					0.4	Nil	6.3	1	6	368		
16J	2¼-9½	L	50	34	16	11.7	0.3	Nil	6.3	3	0	124	24	QS,QC
16J	9½-16+	CL	39	24	37	8.7	0.6	Nil	6.5	3	0	124	35	QS,L,SH
17J	½-1½	Humus					0.4	Nil	6.8	2	4	264		
17J	1½-4	L	50	34	16	12.5	0.4	Nil	6.8	1	0	230	18	QC,QS,L
17J	4-18+	SL	53	28	19	9.4	0.4	Nil	6.6	1	0	116	22	QS,QC
18J	1-1½	Humus					0.4	Nil	6.8	1	11	204		
18J	1½-8	SL	61	28	11	14.5	0.4	Nil	7.6	1	0	352	5	QC
18J	8-18	SL	63	26	11	9.6	0.3	Nil	6.9	1	1	128	21	QC,QS
19B	½-1	Humus					0.5	Nil	7.4	1	11	424		
19B	1-4½	L	45	37	18	15.9	0.5	Nil	7.0	1	3	400	22	L,Q
19B	4½-12	L	41	46	13	17.3	0.3	Nil	7.6	1	0	166	7	L,Q
19B	12-18+	L	44	36	20	19.8	0.5	High	7.9	2	0	90	40	L,Q
20B	½-1½	Humus					0.3	Nil	7.2	1	3	206		
20B	1½-4	L	46	36	18	13.8	0.5	Nil	6.7	0	0	304	5	L,Q
20B	4-6½	L	50	29	21	10.5	0.5	High	7.6	0	0	256	13	L,Q
20B	6½-18	SL	52	32	16	15.3	0.5	High	8.0	1	1	88	48	L,Q
21W	1½-4½	Humus					0.4	Nil	6.1	1	16	218		
21W	4½-8	L	46	31	23	12.4	0.4	Nil	6.6	1	0	98	13	SH
21W	8-14	CL	37	33	30	13.8	0.3	Nil	7.1	0	0	130	21	SH,QS
21W	14-24+	CL	28	39	33	16.0	0.3	Nil	7.3	1	0	158	34	SH,L,Q

NOTES:

[a] Sample lost

[b] + indicates depth of pit profile, not lower depth or horizon

[c] Texture Classes: L = Loam, SL = Sandy Loam, LS = Loamy Sand, CL = Clay Loam, SCL = Sandy Clay Loam, StL = Silty Loam; using the classification of the U.S. Department of Agriculture

[d] Rock Types: QC = Quartz-Feldspar Conglomerate, QS = Quartz-Feldspar Sandstone, Q = Quartzite Sandstone, L = Limestone or Dolomite, SH = Shale, SL = Slate (Shaly)

[e] Available Nutrients: N = Nitrogen, P = Phosphorus, K = Potassium.

prominence indices were *Abietinella abietina* (8), *Hypnum revolutum* + *Drepanocladus uncinatus* (7; combined), *Tortula ruralis* (4), *Pleurozium schreberi* (2) and *Rhytidium rugosum* (2). *Hypnum* and *Drepanocladus* were confused in the field; therefore their values for cover and Frequency were combined.

Abietinella, *Rhytidium* and *Pleurozium* were found frequently in association with *Hylocomium* in a thick feather moss carpet over humus; such carpets were usually restricted to shaded and moist habitats. *Abietinella* was very prominent in Stand 12J and *Rhytidium* in Stand 19B, with indices of 105 and 29 respectively. *Abietinella* had a wider habitat tolerance than the other feather mosses; it occurred with *Drepanocladus* and *Hypnum*, in thin mats on humus, mineral soil or rocks.

Tortula, a turf moss, was recorded in 18 of the 21 stands, and was especially prominent in Stands 4J, 6J and 10B. It appeared most frequently on bare, dry, mineral soil and thick, dry needle litter under heavy shade. Apparently it can tolerate extremes of dessication and poor light intensity better than most other mosses.

Tortula, *Abietinella*, *Hylocomium* and *Hypnum* all had Presence values of over 80%, and can therefore be regarded as constants in the mature Douglas fir ecosystem of Banff and Jasper (Table 16, pp. 112 - 117).

Another 17 mosses and 4 liverworts were recorded but all were infrequent or rare. Five of these mosses were found only in Stand 21W at Waterton: *Lescuraea*

radicosa, *Camptothecium aureum*, *Mnium spinulosum*, *M. lycopodioides* and *Dicranum scoparium*. Their combined influence, together with the complete absence of *Hylocomium*, *Abietinella* and many of the other common mosses in Banff and Jasper, made the bryophyte stratum of this stand unique in this study.

Lichens

The mean total lichen cover was only 4.6%, varying from a maximum of 13.3% in Stand 13J to zero in Stands 9B and 21W. Most of the lichen cover in stands with high totals was composed of species of *Peltigera*. For example, in Stands 8B, 11B, 13J, 14J and 16J, 79% of the total lichen cover was contributed by this genus.

The most frequent of the *Peltigera* species was *P. canina* var. *rufescens*, although typical *P. aphthosa* and *P. aphthosa* var. *variolosa* were both common. Varieties of *Peltigera canina* usually predominated on dry, exposed, south-facing slopes; those of *P. aphthosa* were most common in moist shady habitats, and associated with feather moss carpets. The diversity of habitats in which the species of *Peltigera* occurred makes it unfortunate that difficulties of identification in the field forced a combined value for *Peltigera* cover.

Species of *Cladonia* were the only other prominent lichens in the ground cover, and were present in all but three of the 21 stands. Many species of *Cladonia* were

present but these were very often in the vegetative state, and no attempt was made to identify them beyond the generic level.

None of the other lichens had cover values exceeding 1% in any stand, and were of low Frequency. Four species of *Parmelia*, together with *Usnea* species, *Letharia vulpina*, and *Physcia* species are corticolous lichens that were abundant on trees, and were frequently found on twigs or logs on the ground.

The other eight lichens, including five species of *Cetraria*, were all found on litter or mineral soil, and were infrequent or rare.

VI DESCRIPTION OF TOPOGRAPHY

The altitudinal range of stands at Banff was approximately 1000 feet wide, starting at 4600 feet in Stand 1B and 19B and ending at 5520 feet in Stand 7B. At Jasper the range was about 600 feet wide from 3390 feet in Stand 3J up to 4000 feet in Stand 17J. The mean elevation of Stand 21W at Waterton was 4870 feet (Appendix 1, p. 266).

In aspect the stands showed great uniformity as 16 of the 19 stands with a measurable slope faced no more than 52 degrees from direct south. Exceptions were Stand 12J (NE), Stand 15J (NW) and Stand 16J (WNW).

The stands could be divided into three groups on the basis of slope angle. The first group (Stands 3J, 4J, 5J, 8B, 11B, 12J and 19B) was situated on level ground or on very gentle slopes. Most of them were either on the tops of dry ridges (Stand 3J) or terraces in the valley bottoms (Stands 4J, 5J, 8B and 19B). Stands 11B and 12J were situated at the base of very gentle slopes and were more mesic than usual for Douglas fir forest.

The second group (Stands 1B, 2B, 7B, 9B, 10B, 17J, 18J, 20B and 21W) was situated on steep slopes, varying but little throughout the stand. These stands were a little less uniform in vegetation cover than the first group due to the marked effect of slight variations

in topography on the vegetation. Mean slopes varied between 10° in Stand 1B to 25° in Stands 7B and 9B.

The third group (Stands 6J, 13J, 14J, 15J and 16J) includes only Jasper stands. The topography was extremely variable, slopes within all five stands varying from nil to 23-35°. Consequently the microenvironment varied considerably from steep, exposed, dry slopes to more mesic, level areas with deeper soils. No two of these stands were topographically alike. For example, Stand 6J is on a series of narrow terraces overlooking the Snake Indian River, Stand 13J on a long, concave, south-facing slope overlooking the Miette River, and Stand 15J is situated near the top of a rocky outcrop in the Athabasca River Valley.

VII DESCRIPTION OF SOILS

Marked differences in the parent materials of the soil profiles between Banff and Jasper require that the two regions be considered separately (Table 21, pp. 133 - 134).

Banff

Stands 8B, 11B and 19B were on thick deposits of glacio-fluvial outwash (Rutter, 1965), the coarser fractions composed of limestone and dolomite with a little quartzite sandstone. Stands 1B, 2B, 7B, 9B and 20B were on ground or lateral moraine (Rutter, 1965), composed predominantly of limestone and dolomite with smaller and variable amounts of quartzite sandstone and shale. In Stand 1B the proportion of sandstone was much greater than in the other four stands, and was equal to that of the calcareous rocks. All eight of these stands had pronounced but irregular caliche deposits at various depths in the mineral profiles. The mineral profiles were poorly-developed, with indistinct horizons, and were topped by a thin but clearly differentiated humus layer never more than 2 inches in thickness.

The profile of Stand 10B was very different from those of the other Banff stands, as the C horizon was composed of shale bedrock at a depth of about 12 inches. No caliche was present due to the complete absence of calcareous rock.

The percentage of coarse gravel and rocks in the profile increased rapidly with depth in all nine Banff stands; the soil pit was usually terminated when a virtually impenetrable layer of large rocks was reached at a depth of 12 to 24 inches. In Stands 1B, 2B and 9B the percentage of gravel in the top mineral horizon was unusually high, probably due to rock fall or the erosion of finer materials by slope wash.

The texture of the 2 mm soil fraction at Banff ranged from loam to sandy loam except for Stand 8B. This stand had loam in the upper horizon merging into a heavy clay loam at about 7 inches (soil classification system is that recommended by Soil Science Department, University of Alberta).

The pH of the mineral soil and humus was neutral to alkaline in all stands at Banff except No. 10B. Values up to 8.0 were recorded in most stands due to the high free lime content; values below 7.0 were recorded only in Stand 11B which had 6.6 and 6.5 in the humus and top mineral horizons. Although this stand had a well-developed caliche layer between 8 and 15 inches with a pH of 7.7, the upper horizons were free of lime possibly due to the leaching action of organic acids percolating from the humus.

Because of its non-calcareous substratum, Stand 10B had pH values close to neutral.

Comparison with average levels for agricultural soils (Soil and Feed Testing Laboratory recommendations)

indicated that available nutrients are very limited in the soils of Banff Douglas fir forests. Available nitrogen was very low to absent, no mineral horizons containing more than 5 lbs per acre. Available phosphorus was also very low or absent in all horizons with the exception of Stand 10B (67 lbs per acre in the mineral profile). Available potassium could be classified as high in the humus, varied from very low to high in the mineral horizons, and therefore did not seem to be as deficient in availability as nitrogen and phosphorus.

Available water, defined as the difference between field capacity and the permanent wilting percentage (Chapter IV, p. 67), showed a wide range of values from a minimum of 6.7% in Stand 11B to a maximum of 18.6% in Stand 1B. Available water in sandy loams was not notably lower than that in loam soils. Stand 10B was again different in that its water availability in the mineral profile was highest at 23.3%.

Jasper

The soil parent materials in Stands 3J, 4J, 5J, 15J and 18J were composed predominantly of quartz-feldspar conglomerates and sandstones in glacial drift of indeterminate thickness. In Stands 15J and 18J bedrock was probably very close to the surface. Stands 13J and 14J were on glacial drift of unknown thickness but probably thin in 13J. This glacial drift was composed of shaley slate together with smaller amounts of conglomerate. Bedrock beneath Stands 6J,

16J and 17J was known to be limestone and shale, but a drift sheet composed of these rocks with some sandstone and conglomerate covered all but a few rocky outcrops.

Stands 6J and 12J were the only ones at Jasper in which free lime was present. The profile of Stand 12J consisted entirely of limestone, and caliche deposits were high; caliche was noted in the lowest mineral horizon of Stand 6J.

Therefore the pH values of the mineral horizons of these two stands were alkaline (7.9 to 8.0), whereas corresponding values in the other nine stands were close to neutral. The pH of the humus showed this same trend, Stands 6J and 12J having values of 7.4 and 7.0, and the other nine stands averaging 6.8.

As at Banff, all profiles were poorly-developed, having indistinct mineral horizons topped with thin humus. The humus was of the 'mor' type at both Banff and Jasper (Eyre, 1963, pp. 29-30), although many of the humus samples from Banff had high alkaline pH values due to the high free lime content throughout the profiles. The humus varied in thickness between 1 and 2¼ inches in thickness and was very clearly differentiated from the underlying mineral horizon.

Soil textures differed little from those at Banff and were either loams or sandy loams. Stand 16J was exceptional for its profile changed from a loam to a clay loam at a depth of nine inches.

The description of nutrient availability in Banff soils applies equally to those of Jasper. However, many of

the non-calcareous profiles at Jasper contained relatively more available phosphorus, suggesting a negative correlation between phosphorus availability and profile alkalinity.

Water availability varied from an exceptionally low value of 3.4% in loamy sand in Stand 15J to a maximum of 22.9% in silty loam in Stand 12J. Except for unusually sandy soils, there was no constant relationship between soil texture and soil water availability. The water availability of the few clay loams was no higher, and in one case lower than that of many loams.

The soil parent materials of Stand 21W at Waterton consisted of a mixture of shale, sandstone and limestone. There was no caliche layer, and the profile became increasingly rocky to a sampled depth of 24 inches. The mineral profile became progressively less acid with depth, and changed from a loam to a clay loam at a depth of 8 inches. The humus horizon was thicker (3 inches) than any stand at Banff or Jasper, and had a very acid pH of 6.1. The available nutrients and water were not notably different from those of Banff or Jasper。

VIII VEGETATION AND ENVIRONMENT

Preceding chapters have described the composition and structure of the primary producer level of the Douglas fir ecosystem in Banff and Jasper and a brief description given of the topography and soils pertaining to this ecosystem. Tentative hypotheses pertaining to vegetation -environment relationships have been advanced in the text of these descriptive chapters. Now it becomes necessary to relate the vegetation to the environment on a quantitative basis.

In considering the relationship between vegetation and environment, it must be realized that the two types of variables have different roles. In the absence of conflicting evidence, it is reasonable to assume that the magnitude of each vegetational attribute is limited directly or indirectly by one or a complex of environmental factors.

Simple Correlation

When all data are in a quantitative form, one of the simplest and most satisfactory methods of correlating vegetation and environment is to calculate the correlation coefficient, "r", between selected pairs of variables (Greig-Smith, 1964, p. 102). This coefficient gives a measure of the degree of association between the variables;

it does not distinguish between accidental, indirect and immediate relationships. For example, an unknown third factor may affect both variables in a similar way, such that their correlation is high. However, this method can give useful information that may permit the recognition of closely associated factor-groupings that will greatly simplify further study by regression analysis.

Computer techniques were used to calculate simple correlation coefficients between all environmental variables (Table 22) and selected vegetational attributes. The vegetational attributes chosen were the ones thought to best represent the total vegetation of the strata, and no attempt was made to correlate environmental factors with the attributes of individual species.

The selected data were punched on IBM cards and correlations made by the IBM 7040 Digital Computer in the Department of Computing Science, University of Alberta, Edmonton. The program used for both the calculation of simple correlation coefficients and multiple regression equations (p. 152) was No. G2011 in the program library of the Department of Computing Science, a full explanation of which can be found in Publication No. 1 of this department (Smillie, 1965). Positive or negative correlation was considered significant at the 5% probability level.

1. Tree stratum

Total density and basal area were chosen as tree

TABLE 22. ENVIRONMENTAL VARIABLES USED IN SIMPLE CORRELATION AND IN MULTIPLE REGRESSION ANALYSIS

1.	(X_{10})[d]	Clay in top mineral horizon[a]
2.	(X_{11})	Sand in top mineral horizon[a]
3.	(X_4)	Clay at 10 inches soil depth[a]
4.	(X_5)	Sand at 10 inches soil depth[a]
5.		Permanent wilting percentage in top mineral horizon[a]
6.		Field capacity in top mineral horizon[a]
7.	(X_{15})	Available water in top mineral horizon[a]
8.		Permanent wilting percentage at 10 inches soil depth[a]
9.		Field capacity at 10 inches soil depth[a]
10.	(X_9)	Available water at 10 inches soil depth[a]
11.		Hydrogen ion concentration in humus
12.		Available phosphorus in humus[c]
13.		Available potassium in humus[c]
14.	(X_{12})	Hydrogen ion concentration in top mineral horizon
15.	(X_{14})	Available phosphorus in top mineral horizon[c]
16.	(X_{13})	Available potassium in top mineral horizon[c]
17.	(X_6)	Hydrogen ion concentration at 10 inches soil depth
18.	(X_8)	Available phosphorus at 10 inches soil depth[c]
19.	(X_7)	Available potassium at 10 inches soil depth[c]
20.		Free Lime, maximum in mineral horizons[b]
21.	(X_1)	Mean Elevation, in feet
22.	(X_2)	Mean Slope Angle, in degrees from horizontal
23.	(X_3)	Mean Aspect, in degrees from due south

NOTES: [a] Variables No's 1 to 10 as a percentage of less than 2 mm fraction

[b] Variable No. 20 given numerical values by assigning an arbitrary scale to the original semi-quantitative values as follows: Very High = 5, High = 4, Medium = 3, Low = 2, Very Low = 1, Absent = 0

[c] In lbs per acre

[d] Independent variable number as in Table 25, p. 158-9

stratum attributes most suitable for comparison with environmental data. Estimation of total cover was discarded because of the discrepancy in the two methods employed (Table 9, p. 94).

Both total density and basal area were positively correlated with the amount of available potassium 10 inches below the ground surface (r = +0.7071 and +0.4531 respectively). They were negatively correlated with the percentage of sand in the top mineral horizon (r = -0.5571 and -0.5916). These correlations suggest that the availability of certain nutrients in the mineral profile may be an important limiting factor in the carrying capacity of the tree canopy. However, lack of correlation with other interrelated edaphic variables such as the percentage clay and the percentage sand 10 inches below the ground surface indicate that this suggestion should be treated with caution.

2. Shrub stratum

Total shrub cover, defined as the sum of the percentage cover of all shrub species, was tested for correlation with attributes of the tree canopy as well as physical environmental factors.

The permanent wilting percentage of the soil at a depth of 10 inches was the only environmental variable to show significant simple correlation with shrub cover (+0.4843). However, several attributes of the tree canopy were negatively correlated with shrub cover: total basal

area (-0.5427), mean height (-0.5494), basal area (-0.5934) and mean DBH of Douglas fir (-0.6155). Apparently shrub cover is far more dependent on attributes of the tree stratum than on physical environmental factors directly.

3. Herb and dwarf shrub stratum

Total herb and dwarf shrub cover, defined as the sum of individual species' cover values, showed correlations with the acidity of the soil, for total herb and dwarf shrub cover was positively correlated with free lime content (+0.4514), and negatively with hydrogen ion concentration at a depth of 10 inches (-0.4823). Bacterial breakdown of organic matter will be limited in an acid soil, thus adversely affecting the nutrient cycling and the physiological balance of the soil.

Herb and dwarf shrub cover was positively correlated with elevation (+0.6338), and negatively correlated with the sand:clay ratio in the top mineral horizon (-0.4996). The latter correlation was expected as sandy soils tend to have low nutrient levels.

There was a negative correlation between herb cover and attributes of the tree canopy: mean age of Douglas fir (-0.5744), mean tree cover (-0.4891). Thus a closed canopy is limiting to the development of most herbs as well as shrubs. However, the cover and importance values of lodgepole pine were positively correlated with herb cover (+0.5543 and +0.5364). Since pine has a more open canopy

than fir or spruce it is suggested that the greater the proportion of pine, the less limiting was the tree canopy to the herb and dwarf shrub stratum.

Another possible interpretation of the pine-herb correlation is that the proportion of pine in the canopy and the cover of the herb and dwarf shrub stratum may be essentially independent of each other but negatively associated with the age of the Douglas fir canopy. Older, more mature fir stands will tend to have a low proportion of pine due to the intolerance of this species to shading and competition, and also poorly-developed understory due to the limiting effects of a heavy, closed canopy. Correlation coefficients between the effective stand age and the importance value of pine ($r = -0.6029$) and the herb and dwarf shrub cover (-0.4935) support this hypothesis.

4. Bryophyte and lichen stratum

There was a positive correlation between total bryophyte cover and slope aspect (number of degrees from direct south) (+0.6928). From this it may be hypothesized that the feather mosses, which constitute the majority of the moss cover, cannot tolerate the greater environmental exposure associated with south-facing slopes. Bryophyte cover and the percentage of sand in the top mineral horizon were negatively correlated (-0.5068).

Bryophyte cover was also positively correlated with tree canopy attributes: total density (+0.6355), total

basal area (+0.7265), effective stand age (+0.2818), importance value of white spruce (+0.6139) and the basal area of Douglas fir (+0.5078). It can be hypothesized that the microenvironment created by a dense tree canopy tends to be more limiting to the herbs and shrubs than to the bryophyte stratum which therefore has a competitive advantage.

Two species of *Peltigera* of widely differing habitat requirements (*P. aphthosa* and *P. canina*) make up the bulk of the terrestrial lichen cover, and therefore no correlations were attempted involving this part of the terrestrial bryophyte and lichen stratum.

Multiple Regression Analysis

Introduction

As stated previously, simple correlation coefficients only give a partial measure of association between pairs of variables, and do not necessarily infer cause-effect relationships. They cannot determine which environmental factors are of major influence on the selected vegetation variable, independent of the simultaneous effect of other factors. Simple correlation, therefore, is inadequate for the ecological objectives sought: to determine which of a complex of environmental factors are of major importance to the mature phase of the Douglas fir ecosystem.

Multiple regression overcomes these difficulties to some extent in the following way. An attribute of the

vegetation can be selected (dependent variable) and related to a list of other variables (independent variables) that are thought to have some influence on its variation, in the form of an equation. These independent variables are introduced into the equation in a step-wise manner depending on the magnitude of their correlation with the dependent variable. The influence of previously included independent variables is removed as each new term is introduced, such that residual variation can be further reduced (Smillie, 1965, pp. 92-95).

In this way, an equation can be built up describing the apparent relative influence of environmental factors on a selected vegetation variable, and each variable can be studied independently of the simultaneous apparent influence of the other environmental factors. Also, it becomes possible to make predictions about the dependent variable from the data on the influential independent variables.

One of the first and most successful applications of multiple regression analysis was by Coile (1946) in determining the soil factors which are most correlated with the site index of pine forest stands in the lower Piedmont of North Carolina.

The multiple regression analysis was carried out using the same computer program (G2011) used to obtain simple correlation coefficients (p. 146). Program G2011 cannot use nil values, so a minimal constant of 0.01 was substituted for each zero in the data.

Selection of Independent Variables

There was unfortunately a maximum limit of 49 independent variables permissible in program No. G2011. It therefore became necessary to select out some of the environmental factors as a preliminary step. Also, no purpose would be served by including more than one representative of each group of closely related factors in the regression analysis. Therefore the matrix of simple correlation coefficients between the available quantitative environmental variables was sorted into highly correlated groups of variables (Table 23). It was considered irrelevant whether these correlations were positive or negative.

Since no climatic data were available for the individual stand sites, the list of environmental variables consisted of 20 edaphic and 3 topographic variables.

The three topographic variables, elevation, slope and aspect, were used as independent variables in all regressions because they were not intercorrelated and apparently independent. Slope angle was recorded in degrees from the horizontal, and aspect in degrees from the direct south. An attempt was made to compensate elevation for the disparity in latitude between Banff and Jasper, using a factor of 100 feet per 15 minutes of latitude (Hopkins, 1938). Thus the mean elevation of each stand was converted, to make it equivalent to that of the most southerly Banff stand. This compensation factor still resulted in a mean difference of about 400 feet in elevation between the higher Banff stands

TABLE 23. MATRIX OF SIMPLE CORRELATION COEFFICIENTS BETWEEN ENVIRONMENTAL VARIABLES

Numbered as in Table 22 and arranged to show relationships. Coefficients abbreviated to two numbers as follows: r = -0.5327 listed as -53; 0 = no correlation at the 10% probability level.

V[a]	16	13	19	22	23	21	15	12	18	7	5	8	9	6	10	4	1	2	3	20	17	14
11	0	0	0	0	0	0	0	0	0	0	-47	-41	-40	0	0	0	0	0	0	-51	0	+77
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
17	0	0	0	0	+44	-44	0	0	0	0	-59	-61	-62	-55	-51	+50	0	+41	0	-62		
20	0	0	0	0	0	+63	-53	0	0	0	+74	+72	+56	0	0	-42	0	0	0			
3	0	0	0	0	0	0	0	0	0	0	+39	0	0	0	0	-69	+58	0				
2	0	0	-65	+44	0	0	0	0	0	-59	-46	-45	-54	-70	-51	+59	-77					
1	0	0	+40	0	0	0	0	0	0	0	+48	+46	+58	+49	+58	-73						
4	0	0	0	0	0	0	0	0	0	0	-57	-47	-56	-46	-54							
10	0	0	0	0	0	0	0	0	+50	+63	+46	+63	+90	+72								
6	0	0	0	0	0	0	0	0	+38	+82	+69	+67	+77									
9	0	0	0	0	0	+40	0	0	0	+50	+70	+90										
8	0	0	0	0	0	+40	0	-39	0	0	+80											
5	0	0	0	0	0	+49	0	0	0	0												
7	0	0	+43	0	0	0	0	0	+52													
18	0	0	0	0	0	0	+67	+39														
12	0	0	0	0	0	0	+77															
15	0	0	0	0	0	0																
21	0	0	0	0	-42																	
23	0	0	0	0																		
22	0	0	-51																			
19	0	0																				
13	+60																					

NOTES: [a] Variable Numbers

and those at Jasper. This difference indicated that either Hopkins' correction factor should have been somewhat greater for this latitude or that the Douglas fir in Banff and Jasper are not in elevationally-equivalent habitat zones.

The 20 edaphic variables formed an intercorrelated complex and it was difficult to divide them into discrete, correlated groups. However, within-complex groups were found that contained variables more related to each other than to variables in other groups (Table 23). One variable from each group was chosen to represent that group as an independent variable in each multiple regression analysis, care being taken to select that variable of most potential influence to the dependent variable in question. For example, it was decided to select the edaphic variable at the 10 inch depth of soil for tree and shrub regressions and at the top mineral horizon for herb and bryophyte regressions, because of differences in the probable depth of optimum root concentration by the respective strata.

One historic variable (effective stand age) was allowed to appear in regressions of the tree canopy attributes to assist in accounting for structural differences between stands on basically similar habitats.

Structural attributes of superior strata were allowed to participate as independent variables in equations of subordinate strata. For example, total density, total basal area, lodgepole pine basal area and light intensity (as a percentage of the intensity in the open) were added

as independent variables to the regressions of shrub attributes, since it was considered that total tree density, basal area and tree cover are biological parts of the environment of the shrub stratum. A full list of independent variables used in the regressions is given in Table 25.

Correlations occur between independent variables in the same regression so that they are independent in name only. For example, available potassium at 10 inches depth and slope angle appearing in all tree and shrub attribute regressions, had an "r" value of -0.5104. However the mode of calculation takes into account any correlation between them (Greig-Smith, 1964, p. 127). Strictly speaking, no environmental factor can be considered independent of all others in an ecosystem. These correlations between apparently unrelated factors may represent similar responses to a third factor.

In many cases, the relationship between dependent and independent variables could not be considered linear, especially where the amounts or intensities of the independent variables approach the limits of tolerance of the species. It was therefore thought advisable to transform the independent variables, and then to include both transformed and untransformed values in the regression as independent variables. The regression analysis then selected out which of these transformations gave the best fit in the regression equation. The non-linear transformations were of the form X^2, X^3 and $\log_{10} X$, with the exception of slope

TABLE 24. UNTRANSFORMED INDEPENDENT VARIABLES USED IN MULTIPLE REGRESSION ANALYSES

Independent Variables	Dependent Variables													
	Y_1	Y_2	Y_3	Y_4	Y_5	Y_6	Y_7	Y_8	Y_9	Y_{10}	Y_{11}	Y_{12}	Y_{13}	Y_{14}
X_1	x	x	x	x	x	x	x	x	x	x	x	x	x	x
X_2	x	x	x	x	x	x	x	x	x	x	x	x	x	x
X_3	x	x	x	x	x	x	x	x	x	x	x	x	x	x
X_4	x	x	x	x	x	x	x	x	x					
X_5	x	x	x	x	x	x	x	x	x					
X_6	x	x	x	x	x	x	x	x	x					
X_7	x	x	x	x	x	x	x	x	x					
X_8	x	x	x	x	x	x	x	x	x					
X_9	x	x	x	x	x	x	x	x	x					
X_{10}										x	x	x	x	x
X_{11}										x	x	x	x	x
X_{12}										x	x	x	x	x
X_{13}										x	x	x	x	x
X_{14}										x	x	x	x	x
X_{15}										x	x	x	x	x
X_{16}					x	x	x	x	x	x	x	x	x	x
X_{17}					x	x	x	x	x	x	x	x	x	x
X_{18}					x	x	x	x	x	x	x	x	x	x
X_{19}					x	x	x	x	x	x	x	x	x	x
X_{20}										x	x	x	x	x
X_{21}														x
X_{22}	x	x	x	x										

TABLE 25. ORIGINAL AND TRANSFORMED VARIABLES FOR MULTIPLE REGRESSION ANALYSIS

	Topographic Variables
X_1	Elevation - mean for stand in feet, corrected for latitude
X_2	Mean Slope - in degrees from the horizontal
X_3	Mean Aspect - in degrees from direct south
	Edaphic Variables
X_4[a]	Clay at 10 inch depth below surface
X_5	Sand at 10 inch depth below surface
X_6[b]	Hydrogen ion concentration at 10 inch soil depth
X_7	Available potassium at 10 inch soil depth
X_8	Available phosphorus at 10 inch soil depth
X_9	Water availability at 10 inch soil depth
X_{10}	Clay in top mineral horizon
X_{11}	Sand in top mineral horizon
X_{12}	Hydrogen ion concentration in top mineral horizon
X_{13}	Available potassium in top mineral horizon
X_{14}	Available phosphorus in top mineral horizon
X_{15}	Water availability in top mineral horizon
	Vegetation Variables
X_{16}	Light, mean as a percentage of light intensity, in the open, immediately outside stand
X_{17}	Density of all trees, in stems per 100 square meters
X_{18}	Basal area of all trees, in square feet per acre
X_{19}	Basal area of lodgepole pine in square feet per acre
X_{20}	Shrub cover, sum of percentage cover of individual species
X_{21}	Herb cover, sum of percentage cover of individual species

TABLE 25. (continued)

Historical Variables

X_{22} Effective stand age, mean age of oldest 25% of Douglas fir sampled.

NOTES: Transformations in the form $Log_{10}X$, X^2 and X^3 on all original independent variables except X_2.

Transformations in the form Cosine X and Sine X on variable X_2.

[a] X_4, X_5, X_9, X_{10}, X_{11} and X_{15} as percentages of less than 2 mm fraction.

[b] X_6, X_7, X_8, X_{12}, X_{13} and X_{14} based on less than 2 mm fraction only.

angle for which the transformations were cosine X and sine X. Transformations are obviously not independent of their original variables; where two or more forms of the original variables appear, they form a synthetic expression of the influence of that variable on the dependent variable.

Multiple Regression Equations

The general form of the regression equation may be given as follows:

$$Y = A + B_1X_1 + B_2X_2 + B_3X_3 \text{ etc.}$$

where X = independent variable

Y = dependent variable

A = equation constant

B = regression coefficient

Regression equations were arbitrarily terminated after the eight most "influential" (mathematically accounting for variation in the dependent variable) independent variables had been determined. The regression coefficients were for the complete equation of eight terms and not for a larger equation reported in abbreviated form (Appendix 6, p. 288).

Multiple regression equations were computed with the following attributes of vegetation structure and population size as dependent variables (Y).

Y_1 Basal area of all trees in square feet per acre

Y_2 Basal area of Douglas fir in square feet per acre

Y_3 Importance value of Douglas fir

Y_4 Basal area of lodgepole pine in square feet per acre

Y_5 Shrub cover; sum of percentage cover of individual species

Y_6 *Shepherdia canadensis*; prominence index

Y_7 *Rosa acicularis*; prominence index

Y_8 *Spiraea lucida*; prominence index

Y_9 *Juniperus communis*; prominence index

Y_{10} Herb and dwarf shrub cover; sum of percentage cover of individual species

Y_{11} *Elymus innovatus*; prominence index

Y_{12} *Arctostaphylos uva-ursi*; prominence index

Y_{13} *Fragaria virginiana*; prominence index

Y_{14} Bryophyte cover; sum of percentage cover of individual species.

The independent variables (Table 25) used in each regression were those appropriate to the stratum occupied by the dependent variable. For example, topographic variables, edaphic variables in the top mineral horizon and all the vegetation variables (X_{16} to X_{21}), as well as all transformations of them were used in the regression of dependent variable Y_{14} (Table 24).

Seven equations were computed using the prominence

indices (Chapter 5, p. 111) of four important shrub species and three important herb species as dependent variables. The prominence indices were the same as those used for descriptive purposes of the subordinate strata, the 1.0 constant additive being retained for reasons of consistency.

For a more complete analysis of the construction of the multiple regression equations, see Appendix 6, p. 288.

Results

1. Tree stratum

Y_1 Total Basal Area (Table 26)

The most influential variables are

1) Log_{10} available potassium at 10 inches soil depth and
2) aspect,

together accounting for 39% of the variation of the mean. The simple correlations of both with total basal area are strongly positive: for log_{10} potassium, r = +0.5031; for aspect, r = +0.5025.

The other six terms making up the equation are (stand age)^3, available phosphorus at 10 inches, log_{10} elevation, sine slope angle, log_{10} clay at 10 inches and

TABLE 26. MULTIPLE REGRESSION EQUATIONS SHOWING THE RELATION BETWEEN FOUR ATTRIBUTES OF THE TREE STRATUM, AND THE EIGHT MOST SIGNIFICANT ENVIRONMENTAL VARIABLES.

Total Basal Area (Y_1)

Equation constant = -1554.8

Var.	R.C.	V.
$Log_{10}X_7$	+95.508	25.31
X_3	+0.35739	13.37
$(X_{22})^3$	$+0.2407 \times 10^{-5}$	5.11
X_8	-0.97930	4.60
$Log_{10}X_1$	+982.11	3.28
$Sin.X_2$	-197.67	3.48
$Log_{10}X_4$	-100.88	6.71
$(X_7)^3$	-0.3858×10^{-5}	5.40

T.V.A. = 67.26

Douglas Fir Basal Area (Y_2)

Equation constant = +335.03

Var.	R.C.	V.
$(X_{22})^2$	$+0.3864 \times 10^{-3}$	20.56
X_3	-0.055706	13.06
$(X_6)^3$	-0.76067×10^{-4}	4.03
$Log_{10}X_9$	-155.79	8.58
$Log_{10}X_7$	-80.808	4.55
$(X_7)^3$	-0.3670×10^{-4}	5.07
$Log_{10}X_3$	+9.8421	3.76
$(X_7)^2$	+0.011061	3.44

T.V.A. = 63.05

Importance Value of Douglas Fir (Y_3)

Equation constant = -515.67

Var.	R.C.	V.
$(X_3)^3$	-0.4617×10^{-4}	21.17
$Log_{10}X_3$	+29.616	15.67
$Log_{10}X_8$	+21.796	12.91
$(X_7)^3$	-0.8612×10^{-5}	11.33
$Log_{10}X_7$	+166.78	11.88
X_8	-1.2197	5.69
$Log_{10}X_{22}$	+234.47	2.88
X_{22}	-0.58205	3.91

T.V.A. = 85.44

Lodgepole Pine Basal Area (Y_4)

Equation constant = +389.37

Var.	R.C.	V.
$Log_{10}X_{22}$	-37.314	37.55
$Log_{10}X_3$	-11.671	13.88
X_6	+0.40160	6.98
$Log_{10}X_5$	-179.85	9.25
$(X_7)^2$	$+0.2459 \times 10^{-3}$	4.66
$Log_{10}X_8$	-4.1707	6.60
$(X_5)^3$	$+0.1157 \times 10^{-3}$	4.46
$(X_3)^2$	$+0.3034 \times 10^{-3}$	0.89

T.V.A. = 84.27

NOTES: Var. = Independent variable number

R.C. = Regression coefficient

T.V.A. = Total variation of the dependent variable accounted for by the regression (%).

V. = Variation of the dependent variable accounted for by the independent variable (%).

(available potassium at 10 inches)^3. The appearance of all three topographical variables indicates that topographic position is very important to the carrying capacity of the tree canopy. Only 67% of the variation is accounted for by the eight terms.

Y_2 Douglas Fir Basal Area (Table 26)

The most influential variables are

1) (stand age)^2 and
2) aspect.

Both variables have strongly positive simple correlation with the dependent variable; "r" values are +0.4534 for (stand age)^2 and +0.4506 for aspect. The other six terms are (hydrogen ion concentration at 10 inches)^3, $\log_{10}$ water availability at 10 inches, $\log_{10}$ available potassium at 10 inches, (available potassium at 10 inches)^3, $\log_{10}$ aspect and (available potassium at 10 inches)^2. Only 63% of the variation of the dependent variable was accounted for by this equation.

Three transformed variables of available potassium at 10 inches appear in the equation and two in the previous one, suggesting that the quantitative status of this cation is important to the Douglas fir ecosystem. Aspect also appears prominently in the two basal area equations: positive correlation with north-facing slopes is indicated

in both cases (for Y_1, r = +0.5042; for Y_2, r = +0.4506).

It is likely that south-facing stands have a more open tree canopy and merge into grassland, whereas the stands facing away from direct south, having a more mesic environment, can support a greater carrying capacity in the tree stratum. Douglas fir, however, is less prevalent in these mesic environments than on relatively xeric south-facing slopes.

Effective stand age also appears prominently in both equations and has a strong positive correlation with Douglas fir basal area (r = +0.4440). It therefore appears that the younger stands of fir are situated on the more south-facing slopes. This suggests that a relatively slow climatic change has been responsible for a gradual change in the optimum aspect for Douglas fir development, and is an indication of the dynamic changes in the distribution of fir that may have occurred subsequent to Pleistocene glaciation.

Y_3 Douglas Fir Importance Value (Table 26)

Each of five variables in the equation, representing three environmental factors, account for over 10% of the variation in Douglas fir importance value. They are

1) $(\text{aspect})^3$,

2) $\log_{10}$ aspect,

3) $\log_{10}$ available phosphorus at 10 inches,

4) (available potassium at 10 inches)^3 and

5) $\log_{10}$ available potassium at 10 inches.

The other three variables are available phosphorus at 10 inches, $\log_{10}$ effective stand age and effective stand age.

The presence of two variables each of aspect, available phosphorus and potassium indicates that they or their respective factor groups have a strong influence on the proportion of Douglas fir in the tree canopy in Banff and Jasper.

An hypothesis, that the older the stand, the higher the proportion of fir seems to be indicated by the appearance of effective stand age in this equation; the simple correlation coefficient between effective stand age and Douglas fir importance value is +0.2599. This equation is much more satisfactory than the previous two insofar as it accounts for 85% of the variation.

Y_4 Lodgepole Pine Basal Area (Table 26)

The most influential variables are

1) $\log_{10}$ effective stand age and

2) $\log_{10}$ aspect.

There is a strongly negative simple correlation coefficient between the dependent variable and $\log_{10}$ effective stand

age ($r = -0.6128$), indicative of the declining importance of pine in older Douglas fir stands. The other six variables are hydrogen ion concentration at 10 inches, $\log_{10}$ sand at 10 inches, (available potassium at 10 inches)^2, $\log_{10}$ available phosphorus at 10 inches, (sand at 10 inches)^3 and (aspect)^2. Of the variation, 84% is accounted for by this equation. Sand at 10 inches appears twice here but is absent from the previous three equations. This suggests that the percentage of sand in the soil is more important to lodgepole pine than to Douglas fir.

To summarize the equations on tree stratum attributes, the most influential of those variables sampled and used in the regression are aspect, available phosphorus at 10 inches depth, available potassium at 10 inches and effective stand age, which account for 24 of the 32 occurrences in the four equations. The first three appear to be important factors limiting the development of the Douglas fir ecosystem. Effective stand age emphasizes the changing structure and composition of this ecosystem with increasing age, with Douglas fir increasing and pine tending to decline in importance. It would seem that the life-span of the pine is considerably less than that of the fir in this ecosystem.

2. Shrub stratum

Y_5 Shrub Cover (Table 27)

The most influential variables are

1) $\log_{10}$ total basal area,
2) $\log_{10}$ total tree density and
3) sine slope angle.

The other five variables were total basal area, $\log_{10}$ available potassium at 10 inches, $\log_{10}$ light intensity, slope angle and available phosphorus at 10 inches. The equation accounts for 90% of the observed variation in shrub cover. It is apparent that shrub cover is primarily associated with attributes of the tree canopy. There is a strongly negative simple correlation with $\log_{10}$ total basal area ($r = -0.6759$), indicative of shrub stratum suppression by a well-developed tree canopy. Slope angle, too, seems important to the shrub stratum. Higher shrub cover on steeper slopes may result from other topographic and edaphic factors which tend to reduce the tree canopy on slopes (for slope angle, $r = +0.3109$; for sine slope angle, $r = +0.3136$).

Y_6 Prominence Index of *Shepherdia canadensis* (Table 28)

The most influential variables are

TABLE 27. MULTIPLE REGRESSION EQUATIONS SHOWING THE RELATION BETWEEN THE COVER OF SUBORDINATE STRATA AND THE EIGHT MOST SIGNIFICANT ENVIRONMENTAL VARIABLES.

Shrub Cover (%) (Y_5)

Equation constant = +103.64

Var.	R.C.	V.
$Log_{10}X_{18}$	-57.601	45.69
$Log_{10}X_{17}$	+23.477	12.08
Sin.X_2	+848.56	12.18
X_{18}	+0.097229	5.84
$Log_{10}X_7$	-6.0988	2.61
$Log_{10}X_{16}$	-0.1726×10^{-4}	2.64
X_2	-14.116	5.71
X_8	-0.069968	3.25

T.V.A. = 90.00

Herb and Dwarf Shrub Cover (%) (Y_{10})

Equation constant = -69.491

Var.	R.C.	V.
$(X_{19})^2$	-0.4114×10^{-2}	43.08
$Log_{10}X_{10}$	+55.340	23.32
$(X_{18})^2$	-0.2199×10^{-3}	12.77
$(X_1)^3$	$+0.3793 \times 10^{-3}$	7.05
X_2	-0.57886	4.25
$Log_{10}X_3$	-3.6305	1.93
$Log_{10}X_{12}$	+4.9115	1.79
X_{19}	+0.59263	2.23

T.V.A. = 96.42

Bryophyte Cover (%) (Y_{14})

Equation constant = -51.469

Var.	R.C.	V.
$(X_{18})^3$	$+0.2515 \times 10^{-4}$	72.77
$(X_3)^3$	$+0.5583 \times 10^{-5}$	14.24
$(X_{18})^2$	-0.8285×10^{-2}	3.34
X_{19}	+0.22197	2.70
X_{14}	+0.18226	1.84
X_{17}	+1.1394	1.21
$(X_{11})^3$	$+0.4622 \times 10^{-4}$	1.32
X_{18}	+0.92971	1.04

T.V.A. = 98.46

NOTES: See TABLE 26, page 163.

TABLE 28. MULTIPLE REGRESSION EQUATIONS SHOWING THE RELATION BETWEEN THE PROMINENCE VALUES OF FOUR MAJOR SPECIES IN THE SHRUB STRATUM AND THE EIGHT MOST SIGNIFICANT ENVIRONMENTAL VARIABLES.

Shepherdia canadensis (Y_6)

Equation constant = -61.362

Var.	R.C.	V.
$(X_6)^2$	$+0.6110 \times 10^{-3}$	22.07
X_{18}	-0.35171	12.59
$(X_{17})^3$	+0.018892	14.46
$Log_{10}X_8$	-2.6083	7.18
$(X_{16})^3$	-0.3266×10^{-4}	6.13
$Log_{10}X_6$	+6.8693	7.61
$(X_7)^3$	-0.1442×10^{-5}	3.51
$Log_{10}X_{18}$	+51.897	2.75

T.V.A. = 76.30

Rosa acicularis (Y_7)

Equation constant = +512.70

Var.	R.C.	V.
$(X_7)^3$	$+0.2037 \times 10^{-5}$	11.85
$Log_{10}X_9$	-596.95	18.92
$(X_{16})^3$	-0.6705×10^{-4}	7.38
$Log_{10}X_{16}$	-3.5063	5.85
X_9	+19.116	3.79
X_8	-0.75525	4.97
X_{18}	-0.16853	7.77
X_1	-1.3581	7.47

T.V.A. = 68.00

Spiraea lucida (Y_8)

Equation constant = -52.581

Var.	R.C.	V.
$Log_{10}X_7$	+0.19580	13.48
$Log_{10}X_{17}$	-405.74	11.74
X_{17}	+57.811	5.04
$(X_{18})^2$	-0.3101×10^{-3}	5.02
$Log_{10}X_4$	+114.81	5.80
X_4	-2.3826	13.85
$(X_{17})^2$	-1.9980	6.53
X_2	+0.27061	6.34

T.V.A. = 67.80

Juniperus communis (Y_9)

Equation constant = +2802.5

Var.	R.C.	V.
$Log_{10}X_{18}$	-363.58	40.28
X_{18}	+1.1311	16.74
$Log_{10}X_7$	-1633.8	11.89
X_7	+17.068	9.55
$(X_7)^2$	-0.067637	3.95
$(X_4)^3$	-0.20668×10^{-2}	3.36
$(X_5)^2$	-0.011356	4.15
$(X_7)^3$	$+0.1075 \times 10^{-3}$	3.20

T.V.A. = 93.12

NOTES: See TABLE 26, page 163.

1) (hydrogen ion concentration at 10 inches)^2,

2) total basal area and

3) (total tree density)^3.

Of relatively minor influence are $\log_{10}$ available phosphorus at 10 inches, (light intensity)^3, $\log_{10}$ hydrogen ion concentration at 10 inches, (available potassium at 10 inches)^3 and $\log_{10}$ total basal area. Only 76% of the variation of the dependent variable is accounted for by this equation. It appears that the most influential factors for this shrub species are tree stratum attributes (for total basal area, r = -0.3297) and soil acidity [for (hydrogen ion concentration at 10 inches)^2, r = +0.4698]. The three topograhic factors have little apparent influence on the population size of *Shepherdia*.

Y_7 Prominence Index of *Rosa acicularis* (Table 28)

The most influential variables are

1) (available potassium at 10 inches)^3 and

2) $\log_{10}$ water availability at 10 inches.

Of lesser influence are (light intensity)^3, $\log_{10}$ light intensity, water availability at 10 inches, available phosphorus at 10 inches, total basal area and elevation. This equation accounts for only 68% of the variation.

Y_8 Prominence Index of *Spiraea lucida* (Table 28)

The most influential variables are

1) $\log_{10}$ available potassium at 10 inches,
2) $\log_{10}$ total tree density and
3) clay at 10 inches.

Of lesser influence are total tree density, (total basal area)^2, $\log_{10}$ clay at 10 inches, (total tree density)^2 and slope angle. Like the other two shrub species regressions, the variation accounted for is quite low (68%).

Y_9 Prominence Index of *Juniperus communis* (Table 28)

The most influential variables are

1) $\log_{10}$ total basal area,
2) total basal area,
3) $\log_{10}$ available potassium at 10 inches and
4) available potassium at 10 inches.

The other four variables are (available potassium at 10 inches)^2, (clay at 10 inches)^3, (sand at 10 inches)^2 and (available potassium at 10 inches)^3. Unlike the equation for the three other shrub species, this equation accounts for a large proportion of the variation (93%).

Total basal area and available potassium appear to strongly influence this dependent variable, accounting

for 86% of its variation between them. Total basal area is negatively correlated with the prominence of *Juniperus* (r = -0.5327), indicating that the growth and population size of this species is adversely affected by a forest of high basal area.

Juniperus is negatively associated with the variables pertaining to available potassium (for available potassium, r = -0.4239; for $\log_{10}$ available potassium, r = -0.5984). The growth of *Juniperus*, then, appears mainly controlled by a few environmental factors, unlike the other three shrub species which are influenced by a much wider range of factors.

3. Herb and dwarf shrub stratum

Y_{10} Herb and Dwarf Shrub Cover (Table 27)

The more influential variables are

1) (lodgepole pine basal area)^2,
2) $\log_{10}$ clay in top mineral horizon and
3) (total basal area)^2.

The other five variables are (elevation)^3, slope angle, $\log_{10}$ aspect, $\log_{10}$ hydrogen ion concentration in top mineral horizon and lodgepole pine basal area.

Nearly all the variation of the mean of the dependent variable is accounted for by this equation (96%).

Lodgepole pine basal area is strongly associated with this stratum (for pine basal area, r = +0.6144; (pine basal area)^2, r = +0.6563), the positive correlation being possibly associated with the relatively thin and diffuse canopy afforded by pine, and consequently improved light and water availability for subordinate strata. The hypothesis that the Presence of lodgepole pine in the tree canopy is positively correlated with increased cover of the herb and dwarf shrub stratum can be tested using a "students t" test. This statistic is designed to test the null hypothesis; in this instance whether two samples can be regarded as drawn from the same statistical population, and can be applied to the herb and dwarf shrub cover in those nested quadrats containing pine and those not containing pine (Greig-Smith, 1964, pp. 34-35). Application of the "t" test to these data yielded a significant difference in the means of the two sets of cover values at the 1% level (t = 4.21, with 462 degrees of freedom). All three topographic factors are included in this equation.

Y_{11} Prominence Index of *Elymus innovatus* (Table 29)

The most influential variables are

1) light intensity,
2) shrub cover,
3) lodgepole pine basal area and

TABLE 29. MULTIPLE REGRESSION EQUATIONS SHOWING THE RELATION BETWEEN THE PROMINENCE VALUES OF THREE MAJOR SPECIES IN THE HERB AND DWARF SHRUB STRATUM, AND THE EIGHT MOST SIGNIFICANT ENVIRONMENTAL VARIABLES.

Elymus innovatus (Y_{11})

Equation constant = +1036.2

Var.	R.C.	V.
X_{16}	-1.4785	29.63
X_{20}	-4.9770	18.46
X_{19}	-1.7792	10.41
$(X_{12})^3$	$+0.6838 \times 10^{-3}$	15.99
$Log_{10}X_3$	-11.153	5.89
$(X_{18})^3$	-0.2533×10^{-5}	4.29
$Log_{10}X_{13}$	-396.03	4.53
$(X_{13})^2$	$+0.2348 \times 10^{-2}$	2.18

T.V.A. = 91.38

Arctostaphylos uva-ursi (Y_{12})

Equation constant = -153.25

Var.	R.C.	V.
X_{19}	+3.1250	40.43
$(X_{20})^2$	+0.34186	18.71
$Log_{10}X_{10}$	+195.10	8.91
X_{16}	+2.5580	14.03
X_{15}	-7.7394	5.22
$(X_{11})^3$	-0.5389×10^{-3}	5.00
$Log_{10}X_3$	-12.632	3.99
$(X_{12})^3$	-0.2942×10^{-3}	1.23

T.V.A. = 97.52

Fragaria virginiana (Y_{13})

Equation constant = +37.968

Var.	R.C.	V.
$(X_{19})^3$	$+0.6241 \times 10^{-4}$	57.96
$(X_{14})^3$	$+0.2985 \times 10^{-4}$	5.43
$Cos.X_2$	-47.262	3.64
$(X_{20})^2$	-0.027912	3.88
$Log_{10}X_{20}$	+1.8565	4.10
$(X_3)^3$	-0.1825×10^{-5}	3.10
$Log_{10}X_{15}$	+10.871	2.36
X_{19}	+0.15001	2.06

T.V.A. = 82.53

NOTES: See TABLE 26, page 163.

4) (hydrogen ion concentration in the top mineral horizon)^3.

Of much lesser influence are $\log_{10}$ aspect, (total basal area)^3, $\log_{10}$ available potassium in the top mineral horizon and (available potassium in the top mineral horizon)^2. About 91% of the variation of the prominence index of *Elymus* is accounted for by this equation, 74% by the first four terms. These eight variables cover a wide range of environmental factors, and consist of three tree stratum, one shrub stratum, one topographic and three edaphic variables, so that the survival and growth of this species seems to be regulated by an environmental complex rather than one or two key factors.

The prominence of *Elymus* is negatively correlated with both light intensity ($r = -0.5443$) and shrub cover ($r = -0.5039$), indicating that this grass is not adversely influenced by shading from the tree canopy as are the major shrub species. Competitive exclusion is evidently a factor in this negative relationship between *Elymus* and the shrub stratum.

Y_{12} Prominence Index of *Arctostaphylos uva-ursi* (Table 29)

Of major influence are

1) lodgepole pine basal area,

2) (shrub cover)^2 and

3) light intensity.

The other five variables are $\log_{10}$ clay in top mineral horizon, water availability in top mineral horizon, (sand in top mineral horizon)^3, $\log_{10}$ aspect and (hydrogen ion concentration in top mineral horizon)^3. Of the variation in the prominence index of *Arctostaphylos*, 97% is accounted for by this equation. The most influential variables include several which seem to control *Elymus innovatus*; the most significant of these is lodgepole pine basal area, with which *Arctostaphylos* prominence is highly correlated (r = +0.6359). This suggests that *Arctostaphylos* is more abundant in forests containing a high proportion of pine, therefore allowing more moisture and light to reach the forest floor, and stimulating the growth of many understory species.

Y_{13} Prominence Index of *Fragaria virginiana* (Table 29)

The most influential variable in this equation is

1) (lodgepole pine basal area)^2.

This variable alone accounts for 58% of the variation, the other seven variables being of lesser significance. They are (available phosphorus in the top mineral horizon)^3, cosine slope angle, (shrub cover)^2, $\log_{10}$ shrub cover, (aspect)^3, $\log_{10}$ water availability in top mineral horizon

and lodgepole pine basal area. These seven variables account for an additional 25% of the variation. A very strong positive correlation is shown with both lodgepole pine variables in the equation [for (lodgepole pine basal area)^2, r = +0.7613; lodgepole pine basal area, r = +0.6680] indicating that *Fragaria*, like *Arctostaphylos*, and to a lesser extent *Elymus*, is strongly influenced by the proportion of pine in the tree canopy. This same relationship is shown for the herb and dwarf shrub stratum as a whole, and it would therefore seem that the standing crop of this stratum is in some way increased by the Presence of this species. Proportionately more light and moisture penetrate through a canopy of pine than through fir or spruce canopies, thus encouraging a more luxuriant growth of the herb stratum.

The three major species of the herb and dwarf shrub stratum are influenced far more by direct or indirect attributes of the tree canopy (eg. light intensity, shrub cover) than by edaphic and topographic attributes.

4. Bryophyte and lichen stratum

Y_{14} Bryophyte Cover (Table 27)

The most influential variables in this equation are

1) (total basal area)^3 and

2) (aspect)^3.

The other six variables, all of relatively minor importance, are (total basal area)^2, lodgepole pine basal area, available phosphorus in the top mineral horizon, total tree density, (sand in the top mineral horizon)^3 and total basal area. Total basal area represented by three variables accounts for 77% of the variation in bryophyte cover. It appears that attributes of the tree canopy are of decisive importance to bryophyte cover, which exhibited strong positive correlations with these attributes (for total basal area, r = +0.7225; for total density, r = +0.6359). It is probable that certain bryophyte species which are normally competitively limited by herbs and shrubs become increasingly abundant when the herb and shrub strata are limited by a heavy tree canopy.

Aspect, too, seems important to the bryophyte stratum; there was a strong positive correlation recorded for (aspect)^3 (r = +0.7355), indicating that a more extensive bryophyte stratum can be expected on the more north-facing slopes, where the radiation load on the ground surface is not great. Almost all of the variation (98%) is accounted for by the equation of bryophyte cover.

To summarize, it appears that the three subordinate strata are strongly but differentially dependent on variables associated with the tree canopy, less so on topography, and much less on those other aspects of the

environment for which data were available. The three variables most closely associated with the four tree stratum regressions (available phosphorus, available potassium and slope aspect) represent only five of the 24 terms in the three subordinate strata cover equations. It is surprising that the shrub cover variable does not appear in the equations pertaining to herb or bryophyte cover, or the herb and dwarf shrub cover variable in the bryophyte cover equation. It appears that these strata do not influence each other as much as might be expected.

It is notable that the shrub and bryophyte strata do not appear to be influenced much by the proportion of lodgepole pine in the canopy.

It appears that the environmental requirements of the three lesser strata are similar insofar as these strata show heavy dependence on attributes of the tree canopy. The percentages of the total variation in the subordinate vegetation dependent variables accounted for by variables pertaining to the tree stratum are as follows:

Shrub stratum cover	66%
Individual species' prominence indices in shrub stratum	34%
Herb and dwarf shrub stratum cover	58%
Individual species' prominence indices in herb and dwarf shrub stratum	68%
Bryophyte cover	81%

The herb and dwarf shrub stratum equations differ from those of other understory attributes in that lodgepole pine basal area played a very prominent role in them.

No generalizations can be made concerning the importance of edaphic and topographic variables because the structural and populational attributes demonstrated great individuality in respect to their chief limiting factors.

It must be stressed that many of the independent variables used in the regression equations represent groups of correlated factors, any one of which may be the primary factor involved. Therefore no direct cause-effect relationships can be inferred simply because a certain variable appears to exert influence on the dependent variable. For example, the appearance of available water at 10 inches in the equation would directly relate to the texture of the soil at that depth, as well as field capacity and permanent wilting percentage, any of which may be a more basic cause. It is also very possible that unsampled environmental factors are actually the major causes of variation in the dependent variable. Therefore this section, relating vegetation to environment, must remain tentative and incomplete. The fact that some equations account for over 90% of the observed variation indicates that most of the influential environmental factors or their correlated associates may have been considered.

The value of these multiple regression analyses

lies not only in the establishment of definite relationships between attributes of the environment and vegetation, but also in suggesting which of the complex of environmental factors may have a major controlling influence on, or functional relationship with each vegetational attribute. Hypotheses derived from these regressions may subsequently be confirmed or disproved by more detailed studies of an autecological nature.

IX ORDINATION OF STANDS

Introduction

Preceding chapters have described the floristic composition, vegetation structure and physical habitats of Banff and Jasper Douglas fir forests and the relations between the forests and their habitats. The sampled stands have been treated as integral parts of the general-ized Douglas fir ecosystem of the Alberta Rockies. This chapter will be devoted to a consideration of the relation-ships between the stands and the interpretation of these relationships in the light of the available data.

As a basic approach to this problem of showing relationships between stands, it was decided to construct a classification based on the similarity of flora and plant population size, in preference to one based on habitat similarity, as available vegetational data were far more comprehensive than environmental data.

This section will treat each stand as a vegetational unit and will attempt to answer questions such as

1) Whether or not the Douglas fir forests studied in Banff and Jasper can be considered as two relatively discrete ecosystems.
2) Whether or not any other vegetational dis-continuities exist, and, if so, what environ-

mental factors are responsible.

To satisfactorily elucidate the vegetational relationships between stands, the method of continuous classification (Bray and Curtis, 1957) was preferred to alternative methods of discrete classification for the following reasons. All stands were initially considered as representative of one ecosystem, basically similar in their physiognomy and their dominance by one tree species, Douglas fir (see Criteria for Stand Selection, p. 44). This basic similarity and the implied continuous variation in composition seemed to favour the ordination approach.

Discrete classification would over-emphasize discontinuities in floristic composition and population structure which might be of only minor importance, caused by slight environmental variations or representing natural dynamic fluctuations in composition. Marked discontinuities between groups of stands would be detected by ordination, and also based on a more objective and comprehensive view of the vegetation complex. The implication of continuous variation in the ordination approach was thought to apply to this study far more than the discontinuous implications of discrete classification (Greig-Smith, 1964, p. 161). The quantitative data available in this study made the ordination approach feasible as well as more appropriate.

An ordination places each stand in relation to one or more axes in such a way that its position conveys

the maximum of information about its composition; distances between the stands are inversely proportional to their similarity. The ordination can then be used as a framework on which any variable can be plotted, for which a value can be assigned to individual stands. Thus, by examination and comparison of the distribution of these variables on the ordination, association between species, or correlation between species populations and environmental variables can be detected, and later verified by statistical methods.

Index of Similarity

The measure of floristic similarity was that used by Bray and Curtis (1957), based on an index of similarity calculated from the formula:

$$\text{Index of similarity} = \frac{200\ W}{A + B} \quad \text{(as a percentage)}$$

where A = Sum of quantitative values (in this case, prominence index) of all species in one stand,

B = Sum of quantitative values in another stand, and

W = Sum of quantitative values the two stands have in common.

The quantitative values for each stand used in the equation were derived from the species population size data.

The prominence index, introduced by Beals (1960), and modified by La Roi (1964), was thought to be the most suitable, single quantitative value obtainable from these data; it was taken as the product of the percentage cover and the square root of the percentage Frequency. Cover was thought to be the most important single criterion of species population size applicable to all strata, while quadrat Frequency, a measure of population pattern in a stand, was used to modify it. It was necessary to use the square root and not the full value of the Frequency to prevent it playing a disportionately large part in the prominence index. Many species had very small cover but comparatively large Frequency.

Minimum possible cover and Frequency values had to be assigned to those species for which estimates of only one or the other were available for a certain stand. Species registered as present in a stand but failing to appear in the Frequency or cover data were assigned prominence indices equivalent to the minimum possible for that stand. For example, a species with a Frequency of 20%, but no recorded cover (of 400 possible cover points) would have a prominence index of $(1/400 \times 100) \times \sqrt{20} = 1.12$; a species appearing on the Presence list for a stand of 20 quadrats and 400 cover points would have a prominence index of $(1/400 \times 100) \times \sqrt{1/20 \times 100} = 0.56$.

A constant of 1.0 was added to the prominence index of each species to give some weight to its Presence

in a stand, irrespective of its cover and Frequency, and to reduce fluctuations in the prominence of rare species based on sampling error. For presentation purposes only, these indices were abbreviated to whole numbers (Table 16, pp. 112-117).

Indices of similarity were calculated for all possible pairs of stands, including Stand 21W at Waterton, using computer techniques and an index of similarity program prepared by Ream (1962)(Appendix 3). Species of the tree, lichen and bryophyte strata were not included in the index of similarity. Tree species were omitted because the criteria for stand selection (p. 44) pre-determined the structure and composition of the tree stratum. Identification of many bryophytes and lichens was only to genus and therefore their cover and Frequency estimates were of reduced value. For this same reason *Salix* spp., *Poa* spp., *Taraxacum* sp. and *Potentilla* sp. were also omitted.

Construction of the Ordination

A two-dimensional ordination was constructed using the indices of similarity and the method of Beals (1960).

So that the distances between stand locations on the ordination would be inversely proportional to their index of similarity, the index was subtracted from an arbitrary value of 85% to give an "index of dissimilarity". This value of 85% was used instead of the theoretical maxi-

mum of 100% for two reasons:

1) Resampling a stand for Frequency and cover at different times, and then calculating indices of similarity between the samples would result in indices considerably below the theoretical maximum of 100% due to sampling variation and periodicity. Based on resampling field trials, Beals (1960) used a value of 85, and Bray and Curtis (1957) used 80.
2) The maximum index of similarity obtained, 83%, was between Stands 4J and 5J. These two stands were very nearly identical in composition, structure and topography and only one-half mile apart. These observations indicated that they should have had an index of similarity very close to 100%, so that sampling error undoubtedly accounts for most of the lower figure.

The stand with the smallest sum of index of similarity values (the most dissimilar stand), was selected as one end of the primary or X axis (Stand 21W). Then the stand with the lowest index of similarity to Stand 21W was chosen as the other end-stand of the X axis (Stand 3J). This X axis was thus 79.25 units long (index of dissimilarity of Stands 3J and 21W = 79.25). The other 19 stands

were located along this axis according to their relative similarity to Stands 3J and 21W, using a formula based on the Pythagorean theorem:

$$X = \frac{L^2 + Da^2 - Db^2}{2L}$$

where L = length of X axis,
Da = index of dissimilarity with Stand 21W,
Db = index of dissimilarity with Stand 3J and
X = distance along X axis from Stand 21W.

The first reference stand on the Y axis was selected as the one whose intersection of arcs (with radii equal to indices of dissimilarity from end-stands on the X axis) was at the greatest distance from the X axis. This distance can be calculated from the formula

$$\sqrt{Da^2 - X^2}.$$

Stand 2B proved to have the largest value. The other end-stand of the Y axis was the one most dissimilar to Stand 2B, and at the same time within 10% of it on the X axis (Stand 7B). This made the Y axis approximately perpendicular to the X axis, and 72.0 units in length. The positions of all stands on the Y axis were then obtained (including Stands 3J and 21W, the ends of the X axis), using the same formula as for the X axis.

The positions of the 21 stands were plotted on

the resulting two-dimensional ordination field, using the values of X and Y for each stand as coordinates (Table 30; Fig. 13A). The Y axis was assumed to be absolutely vertical, for convenience in plotting positions.

The ordination using all 21 stands proved to be unsatisfactory because Stand 21W (Waterton) was so dissimilar to the other 20 that the latter became bunched at one end of the X axis. It was obvious that the Presence of Stand 21W hindered the accurate separation of stands, thereby obscuring any groupings which may have existed among the other stands.

This was strong proof that the floristic composition of the Waterton stand was so different from any of the stands at Jasper and Banff that it should be discarded for purposes of ordination.

Therefore a second ordination was prepared in the same manner as the first, except that Stand 21W was omitted (Table 30; Fig. 13B). In this ordination the first and second end-stands of the X axis were Stands 2B and 5J, and those of the Y axis were Stands 10B and 15J. The lengths of the X and Y axes were 72.2 and 62.5 units respectively. The second ordination was used for subsequent detection of association between species or correlations between species populations and environmental variables.

TABLE 30. LOCATION OF STANDS ON ORDINATION

Stand	Ordination Including Stand 21		Ordination Excluding Stand 21	
	X axis	Y axis	X axis	Y axis
1B	13.7	9.8	10.1	37.3
2B	22.4	0	0	34.1
3J	0	48.4	54.7	41.1
4J	6.2	64.6	67.9	35.7
5J	1.6	67.6	72.2	32.6
6J	12.7	42.9	47.0	34.0
7B	15.3	72.0	67.4	56.0
8B	14.3	32.0	18.0	48.2
9B	21.4	30.4	23.5	43.9
10B	13.7	60.0	51.2	62.5
11B	11.7	38.2	27.5	61.9
12J	9.5	61.2	67.5	27.4
13J	12.1	50.1	57.8	26.5
14J	19.0	61.1	63.0	32.2
15J	17.9	40.9	52.4	0
16J	22.2	19.7	19.4	24.0
17J	8.6	59.0	65.1	36.0
18J	9.0	50.0	61.3	26.7
19B	13.4	36.5	24.0	53.2
20B	18.6	19.7	9.7	45.4
21W	79.3	40.6		

FIGURE 13. LOCATION OF STANDS ON THE ORDINATION

Using:

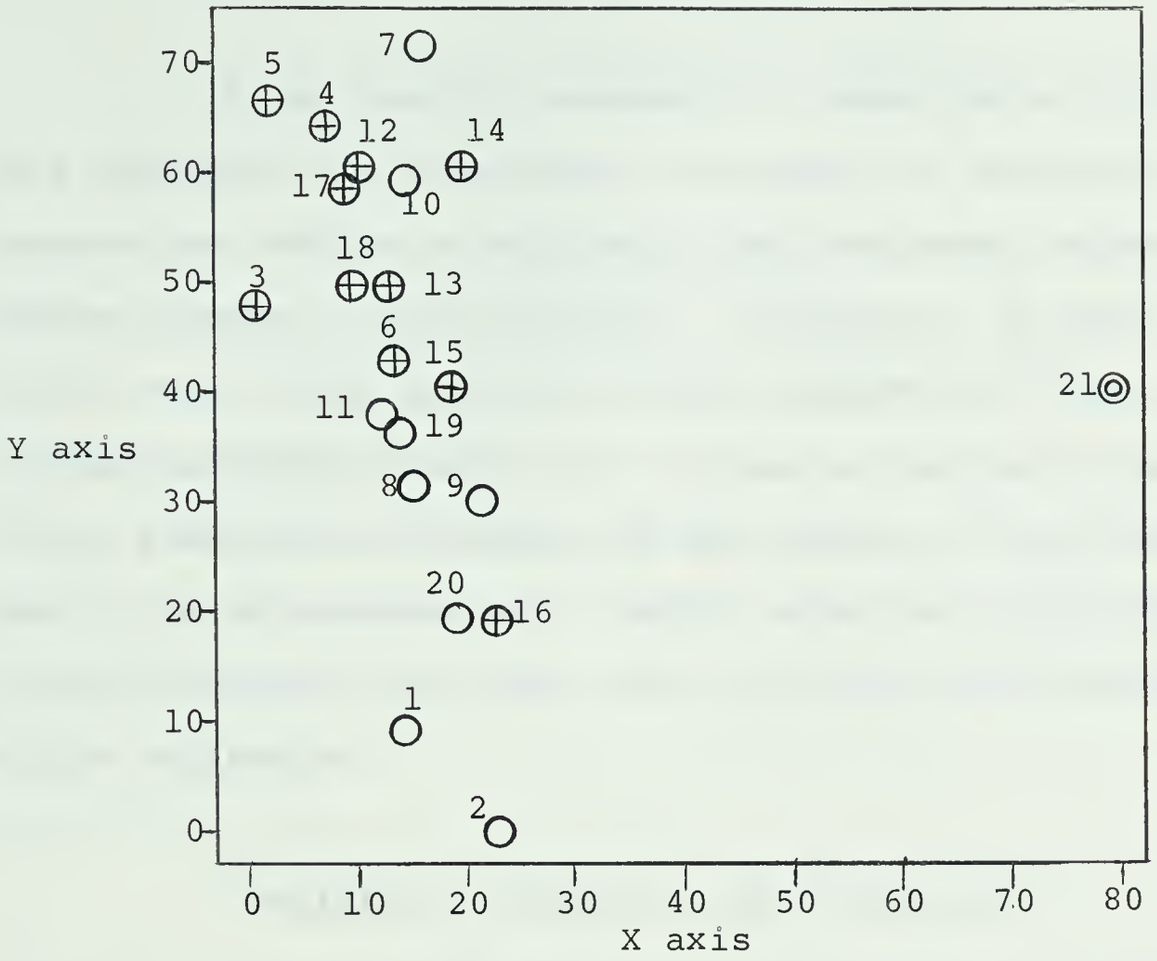
A. All 21 stands

B. 20 stands only (excluding stand No. 21)

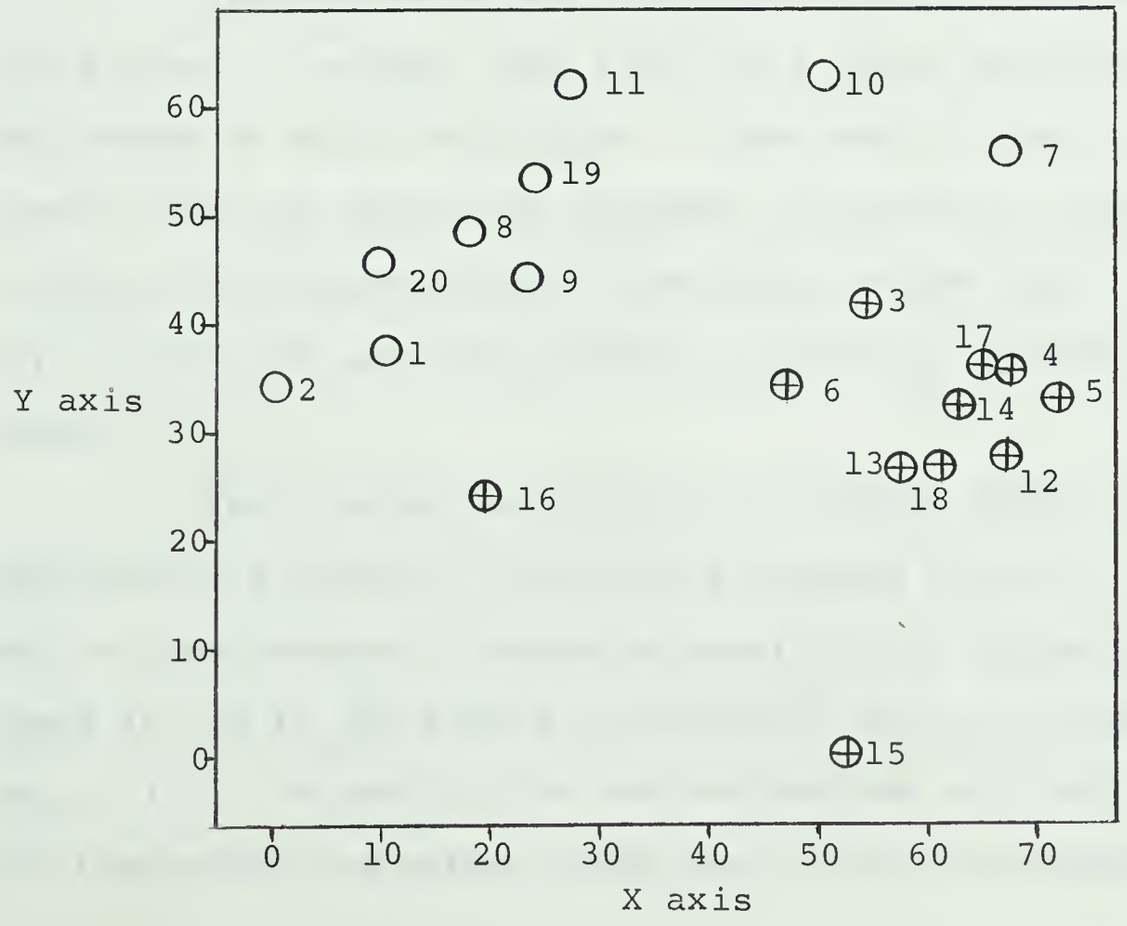
Banff stands shown with hollow circles, Jasper stands with crossed circles and the Waterton stand (No. 21) with a double circle. Numbers of stands correspond to those on maps (Figs. 2 and 3), and are in chronological order.

FIGURE 13

A. Ordination of all 21 stands



B. Ordination of 20 stands only (excluding No. 21)



Validity of Ordination

It was thought necessary to check the validity of this ordination by determining the degree of correlation between the indices of similarity and the actual distances between stands on the ordination. Therefore, 40 pairs of stands were chosen at random (from a maximum of 178), and a simple correlation coefficient calculated between inter-stand ordination distances and the indices of similarity. The 'r' value obtained was -0.8021, which was significant at the 1% probability level, thus confirming the validity of the ordination.

Position of Stands on the Ordination

Inspection of the stand positions on the ordination field makes it evident that there is a clear division between the stands at Banff and Jasper. Seven Banff stands are spread over the upper left quadrant, whereas ten Jasper stands are clustered at the right side of the field. Stands 7B, 10B and 16J are intermediate in position between these groups.

The 21-stand ordination (including Stand 21W) obscures this bimodal relationship because Stands 7B, 10B and 16J are located in opposite geographical groupings; Stand 16J is in the middle of the Banff group of stands (Fig. 13A). In reality the two ordinations are very similar, but the second one makes better use of the two dimensions.

The first ordination appears to use little more than one dimension due to the great floristic differences between Stand 21W and the other 20.

Distribution Patterns of Quantitative Variables on the Ordination

1. Tree stratum (Fig. 14)

Total basal area and total tree cover are at a maximum in the right center part of the ordination field (in Stands 4J, 5J, 12J, 13J, 14J, 15J, 17J and 18J at Jasper, and 7B at Banff). The pattern of total basal area is less defined than that of total cover.

Douglas fir basal area and height maxima coincide with those of total basal area and total tree cover, indicating that Douglas fir is responsible for the greater standing crop of those stands in the right center of the field.

In contrast, lodgepole pine basal area reaches a maximum in the upper left part of the ordination field (in Stands 2B, 8B, 11B and 19B at Banff, and 16J at Jasper).

The pattern of effective stand age is essentially the same as that of the attributes of Douglas fir and the total tree cover. Therefore, the standing crop, as indicated by total basal area, is fairly uniform, but relative amounts contributed by fir and pine differ according to stand age.

FIGURE 14. PATTERNS OF SIGNIFICANT, QUANTITATIVE, TREE STRATUM ATTRIBUTES ON THE ORDINATION OF 20 STANDS

A. Total Basal Area: progressively larger cirles represent classes of less than 60, 60 - 100, 100 - 140, 140 - 180 and more than 180 square feet per acre.

B. Douglas Fir Basal Area: size of circles as for Total Basal Area.

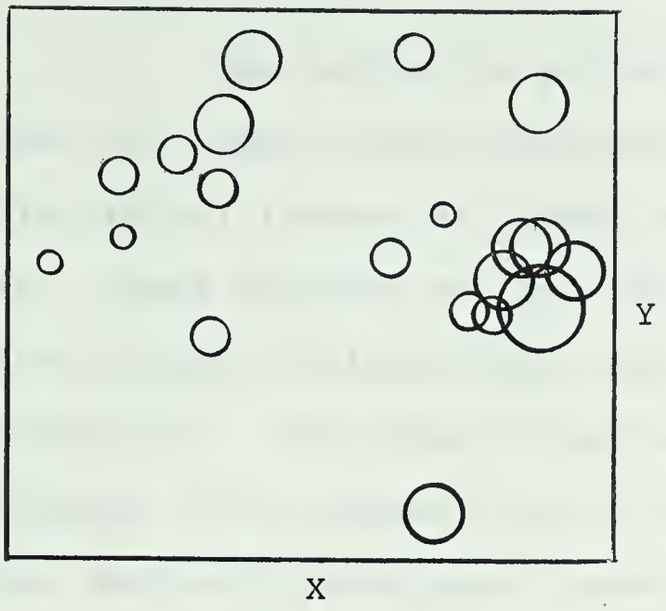
C. Lodgepole Pine Basal Area: progressively larger circles represent classes of less than 10, 10 - 20, 20 - 30, 30 - 40 and more than 40 square feet per acre.

D. Total Cover; from cover-point data: progressively larger circles represent classes of less than 30, 30 - 40, 40 - 50, 50 - 60 and more than 60 percent.

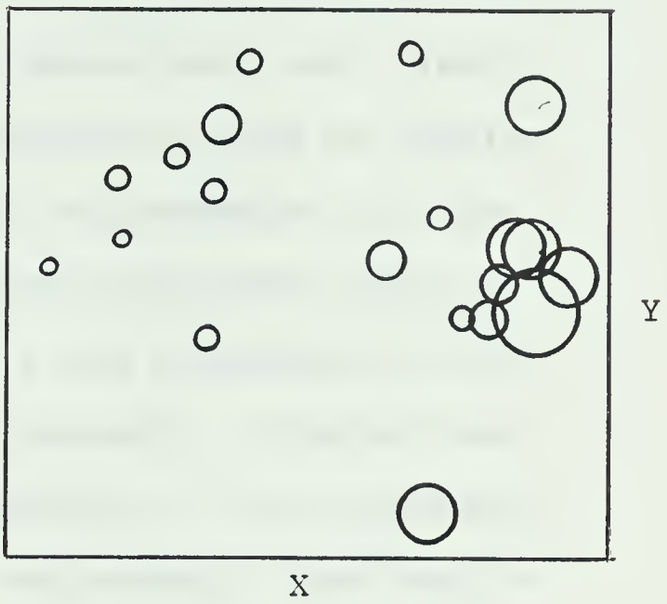
E. Effective Stand Age; the mean age of the oldest 25% of trees sampled in the stand: progressively larger circles represent classes of less than 80, 80 - 160, 160 - 240, 240 - 320 and more than 320 years.

F. Douglas Fir Height; the mean height of the tallest 25% sampled: progressively larger circles represent classes of less than 55, 50 - 70, 70 - 85, 85 - 100 and more than 100 feet.

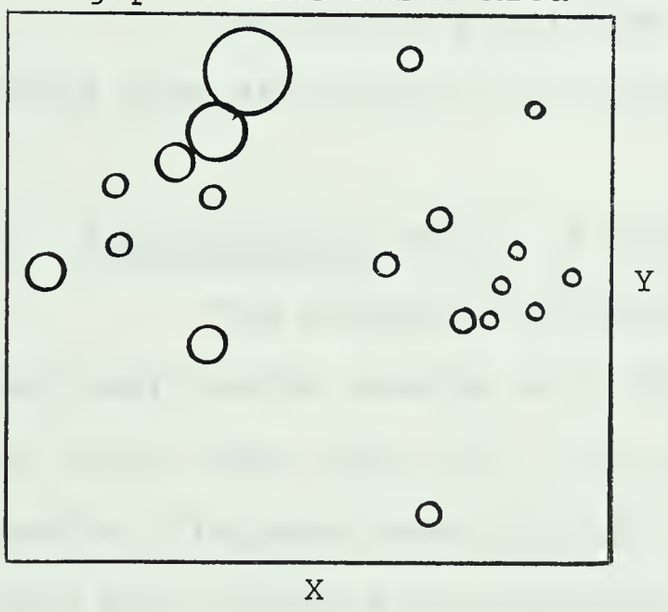
Total Basal Area



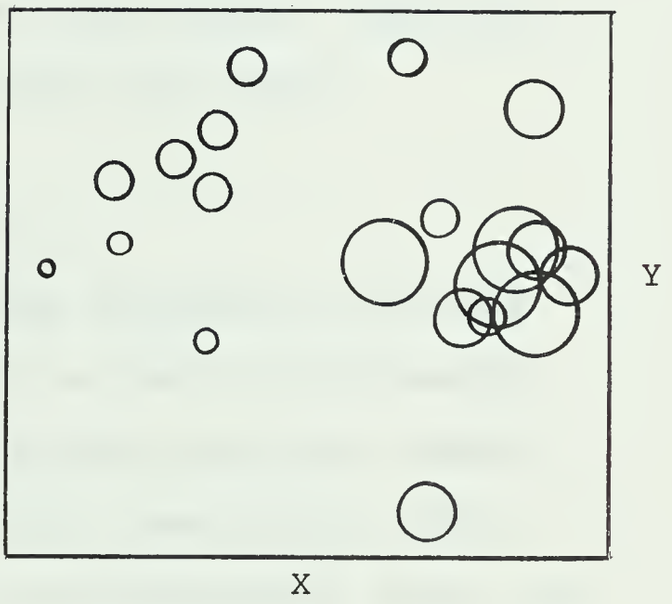
Douglas Fir Basal Area



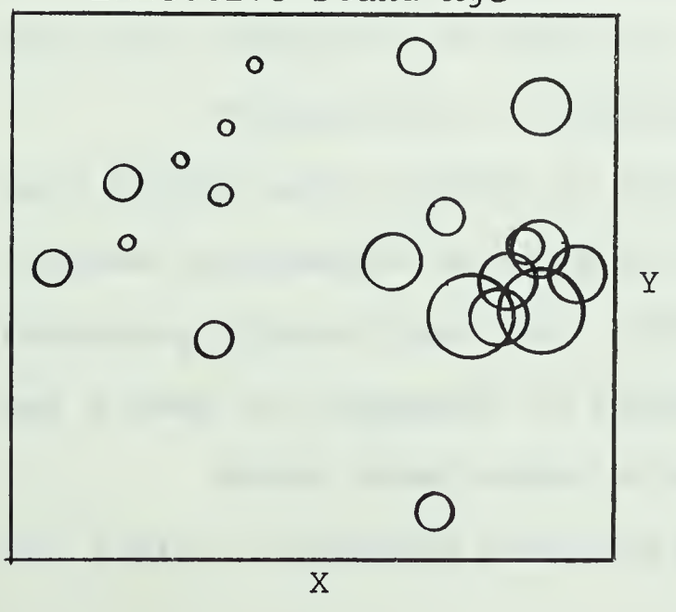
Lodgepole Pine Basal Area



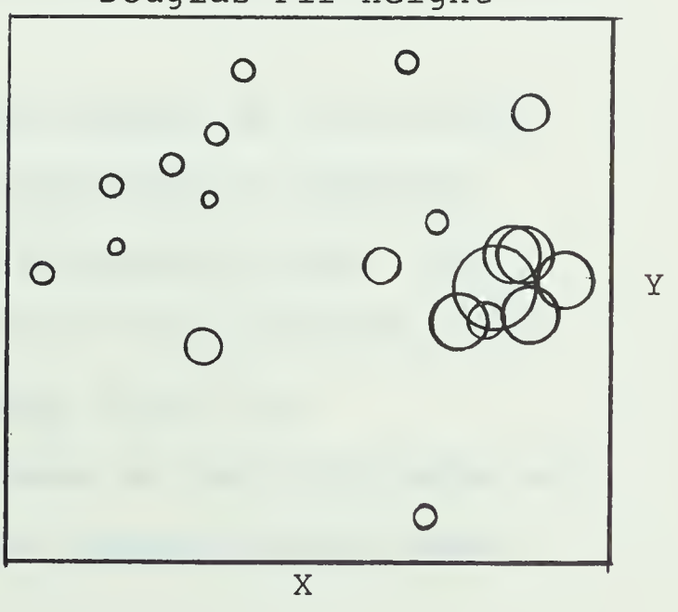
Total Cover



Effective Stand Age



Douglas Fir Height



The ordination patterns demonstrate very clearly that the older, taller, heavier-canopied stands of Douglas fir are all located at Jasper with the exception of Stand 7B. These patterns are all the more significant since no tree canopy attributes were used in the preparation of the ordination. From this it may be reasonably inferred that changes in the composition and abundance of the understory are obviously paralleled closely and probably regulated by changes in the tree canopy.

Attributes pertaining to white spruce, aspen and total tree density did not demonstrate any trend.

2. Shrub stratum (Figs. 15 and 16)

The abundance of the shrub stratum and the herb and dwarf shrub stratum as a whole can best be represented by total cover (Fig. 16). For individual species, however, quadrat Frequency was selected as the quantitative attribute most suitable for plotting on the ordination (Fig. 15); cover values generally have too narrow a range, and density data are inadequate or lacking.

Frequencies of prominent species in the subordinate strata were entered on the ordination in Frequency classes represented by circles of decreasing size. The Frequency classes used were 100-76%, 75-51%, 50-26%, 25-1% and a dash to represent no Frequency (Fig. 15).

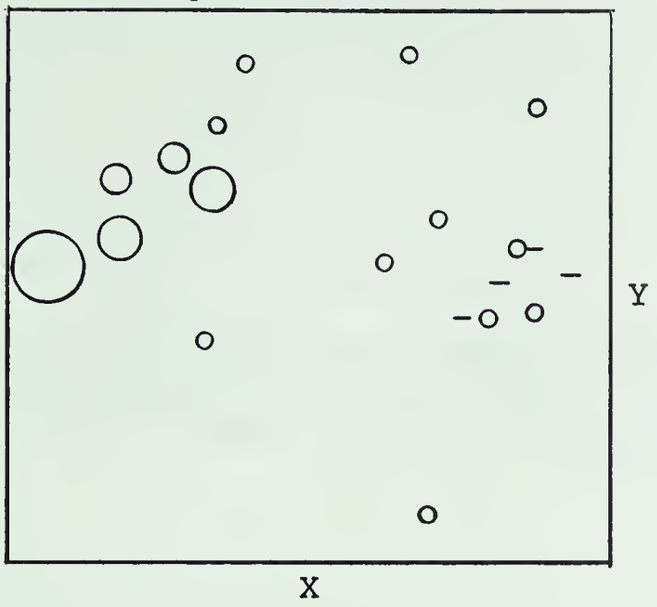
Shrub cover shows a maximum in the left center of the field, indicating that the most abundant shrub cover

FIGURE 15. QUANTITATIVE PERFORMANCE OF SIX SHRUB SPECIES ON THE 20-STAND ORDINATION

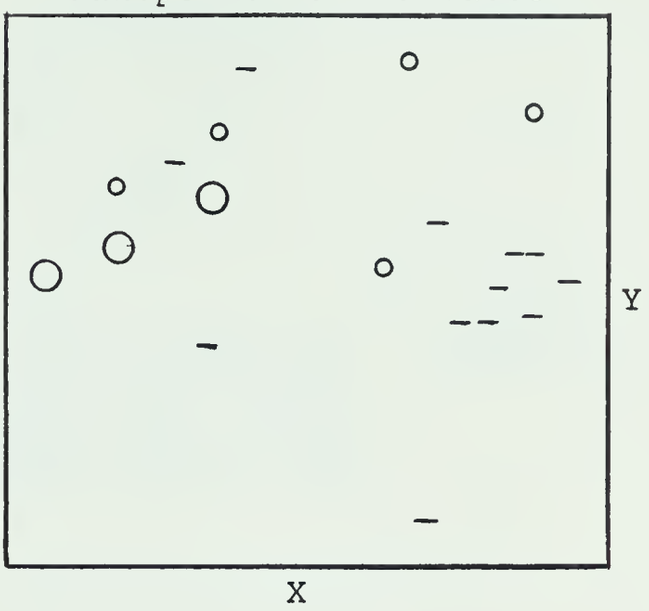
Progressively larger circles represent classes of 1-25, 26-50, 51-75 and 76-100% quadrat Frequencies.

No Frequency represented by a dash.

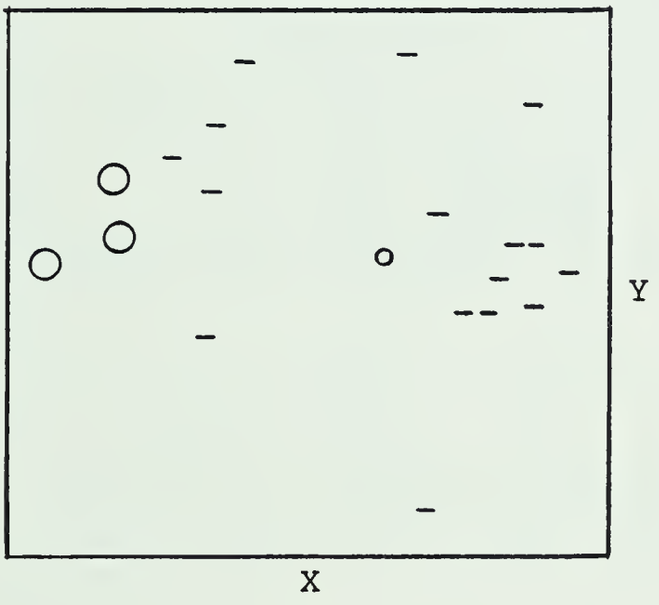
Juniperus communis



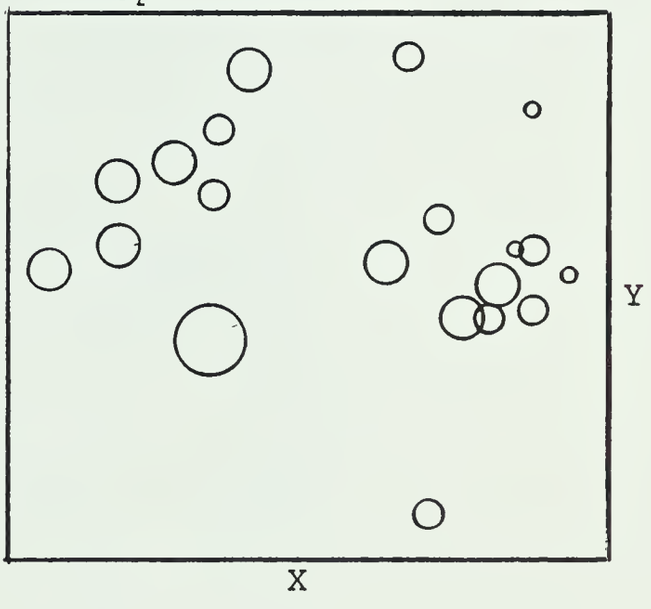
Juniperus horizontalis



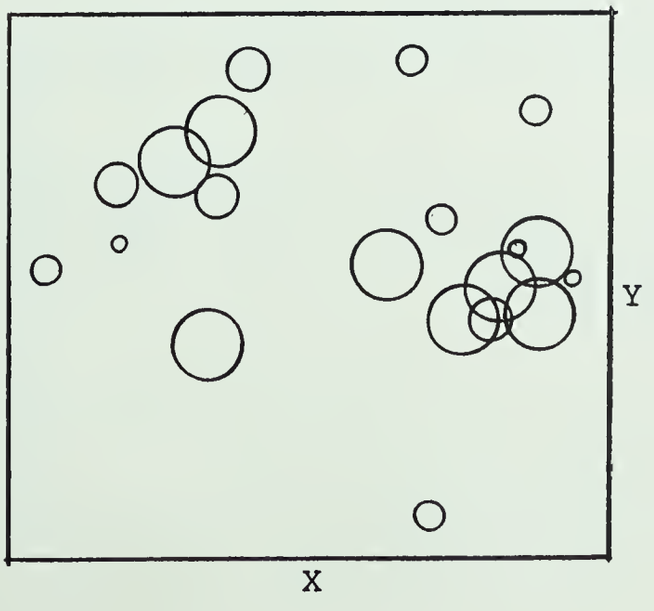
Rosa woodsii



Shepherdia canadensis



Rosa acicularis



Spiraea lucida

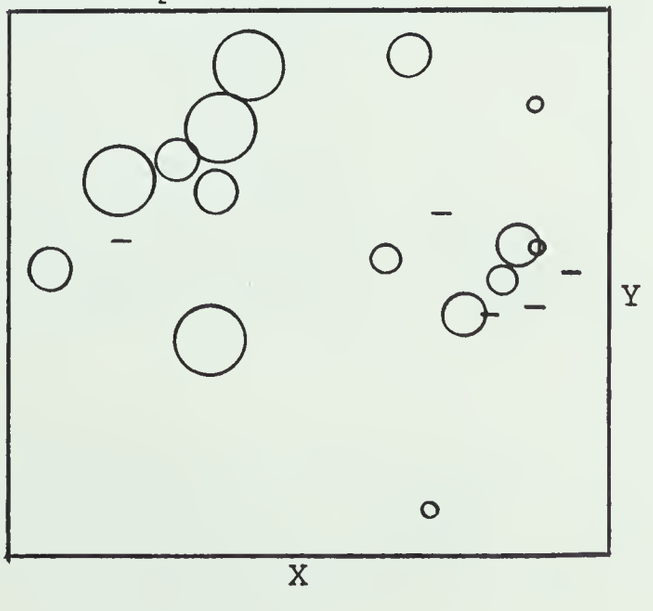


FIGURE 16. PATTERNS OF TOTAL SHRUB COVER, *ROSA ACICULARIS* COVER, HERB AND DWARF SHRUB COVER, *SENECIO CANUS* PRESENCE AND *SENECIO CYMBALARIOIDES* PRESENCE ON THE 20-STAND ORDINATION

Total Shrub Cover: progressively larger circles represent classes of less than 1, 1 - 3, 3 - 5, 5 - 10 and more than 10 percent cover.

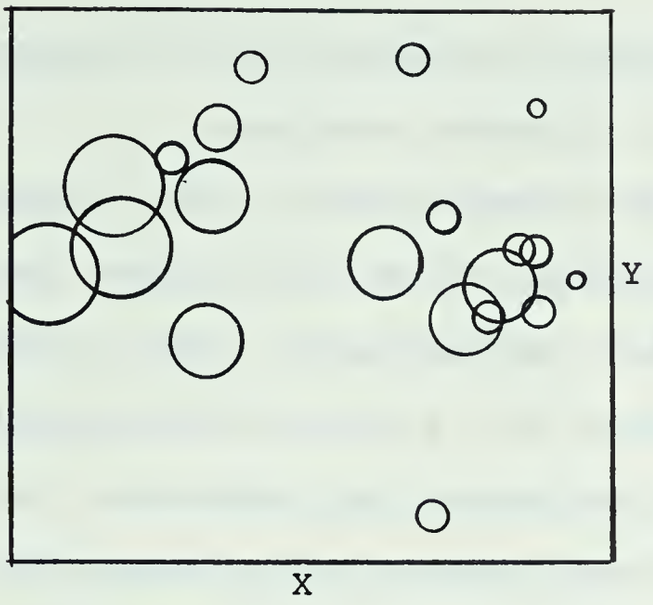
Rosa acicularis Cover: progressively larger circles represent classes of less than 1, 1 - 3, and more than 3 percent cover; no cover represented by a dash.

Herb and Dwarf Shrub Cover: progressively larger circles represent classes of less than 10, 10 - 20, 20 - 30, 30 - 40 and more than 40 percent cover.

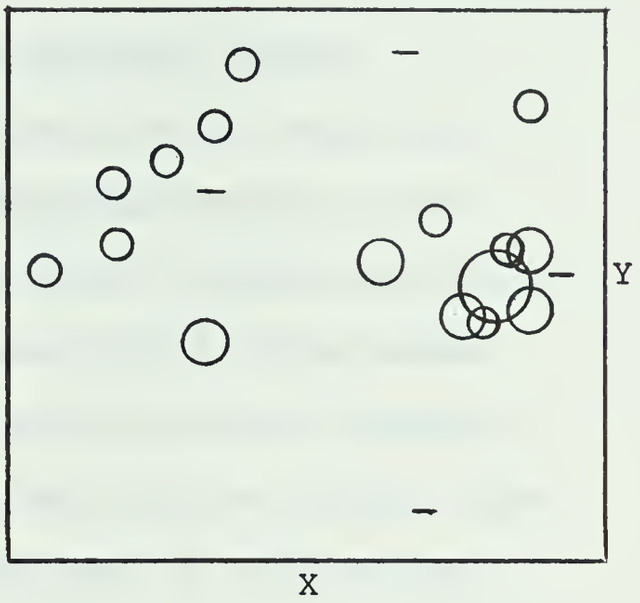
Senecio canus Presence: circles represent Presence in the stand; dashes represent absence from the stand.

Senecio cymbalarioides Presence: symbols as for *Senecio canus* Presence.

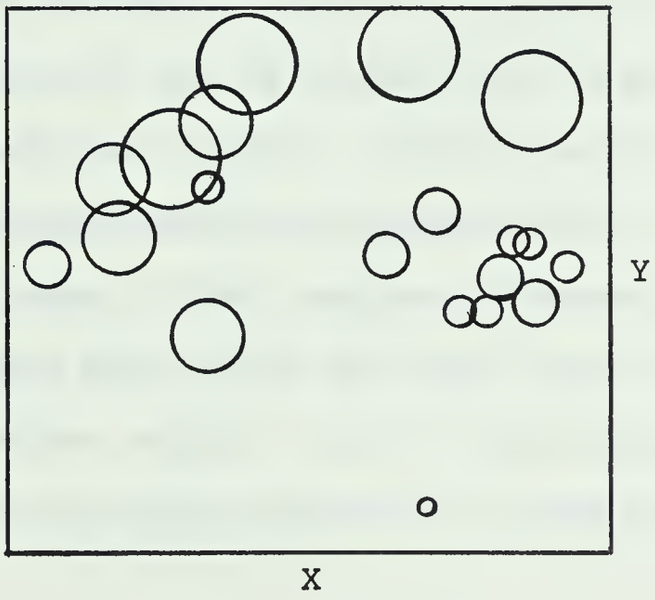
Total Shrub Cover



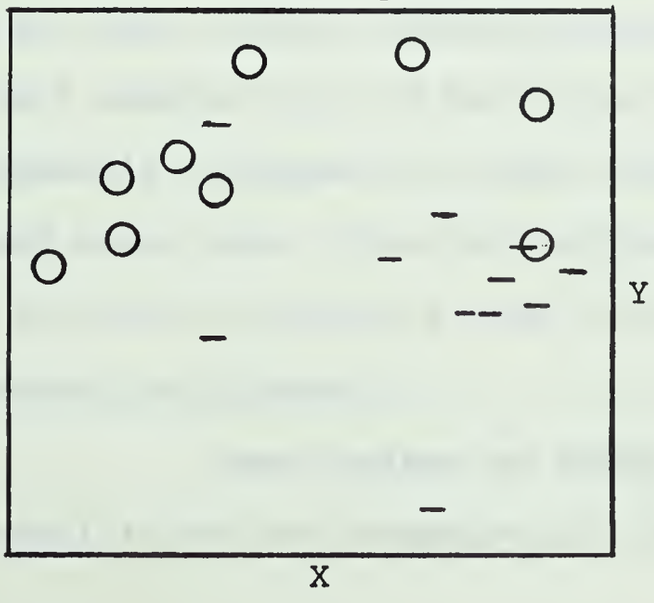
Rosa acicularis Cover



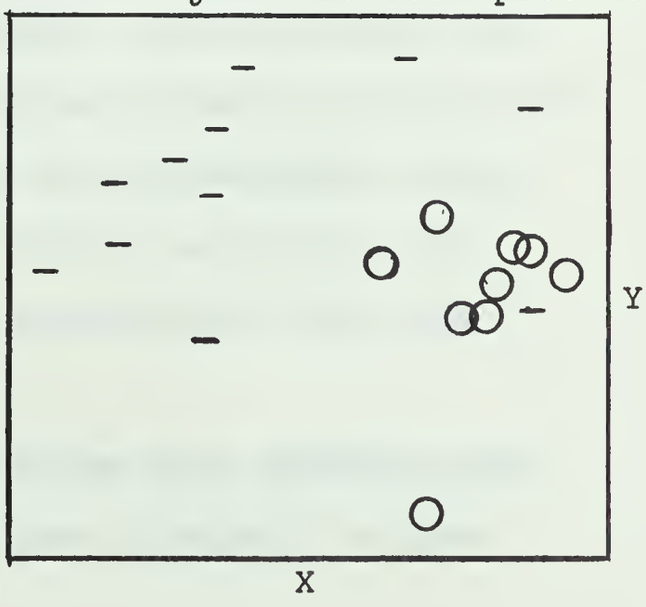
Total Herb and Dwarf Shrub Cover



Senecio canus -presence



Senecio cymbalaroides -presence



occurs in the younger and lighter-canopied stands.

Juniperus communis, *J. horizontalis* and *Rosa woodsii* form closely-associated Frequency maxima in the left center part of the ordination field (Stands 1B, 2B, 9B and 20B). Supplementary 2x2 contingency table tests (Greig-Smith, 1964, p. 39) on 4x4 meter quadrat Presence data supported the recognition of this species group. The Chi-square value obtained from each pair of species was referred to a Chi-square table (Snedecor, 1956, pp. 28-29) with one degree of freedom. *Juniperus communis* showed positive association at the 1% probability level with both *J. horizontalis* and *Rosa woodsii*, indicating that these three species have very similar requirements in this part of their habitat range. Their maximum Frequencies coincided with minimum basal area and tree cover areas on the ordination, strong support for the hypothesis that *Juniperus communis* is very susceptible to exclusion by shading.

The Frequencies of the other three shrub species have more diffuse ordination patterns. *Spiraea lucida* is more abundant on the Banff part of the ordination field and generally uncommon in those stands with high canopy cover and basal area. The ordinations of *Rosa acicularis* and *Shepherdia canadensis* show little association with tree canopy attributes.

Cover values of shrub species were generally too small (with the exception of *Juniperus communis*) to show

much when plotted on the ordination. The cover of *Rosa acicularis*, however, showed a maximum in the right center of the field, in the more mature Douglas fir stands. Of the shrub species studied, *Rosa acicularis* can best tolerate the lower light intensities and possibly poorer moisture conditions associated with mature, closed canopy fir forest.

To detect association between *Shepherdia*, *Spiraea* and *Rosa acicularis*, 2x2 contingency table tests were made (Greig-Smith, 1964, pp. 39-40) on 4x4 meter quadrat Presence data. These tests showed that the three species are all positively associated at the 1% probability level, indicating that their habitat requirements are very similar, although it has been shown that their tolerance to shade and associated environmental limitations are slightly different (*Spiraea* least tolerant; *Rosa acicularis* most tolerant).

The six shrub species seem to represent a trend from *Rosa acicularis* with high Frequency and wide tolerance to environmental variation to *Juniperus communis* with relatively low Frequency and a restricted distribution due to a narrow tolerance range. Ordination has clarified considerably the phytosociological relationships of these shrub species within the Douglas fir ecosystem.

3. Herb and dwarf shrub stratum

Herb and dwarf shrub stratum cover shows a pronounced maximum in the upper left part of the ordination

field (Fig. 16). As noted earlier, the proportion of lodgepole pine in the tree stratum peaks in the same part of the ordination field (p. 194). The negative correlation between the cover of the herbs and dwarf shrubs and the total basal area of the tree stratum is also clearly shown on the ordination.

The quadrat Frequencies of nine prominent species of the herb and dwarf shrub stratum were plotted on the ordination (Figs. 17 and 18). Six of them, *Arctostaphylos uva-ursi*, *Aster laevis*, *Astragalus decumbens*, *Festuca scabrella*, *Hedysarum sulphurescens* and *Solidago decumbens* show a maximum population size in the upper left quadrant of the field (in Stands 1B, 2B, 8B, 9B, 11B, 19B and 20B). Supplementary evidence that the six form a closely associated group was obtained from 2x2 contingency table tests of association between them, using 1x1 meter quadrat Presence data from the Banff stands. All possible paired combinations were positively associated at the 1% probability level except the three following combinations which showed no association: *Aster laevis* with *Astragalus decumbens*, *Festuca scabrella* and *Hedysarum sulphurescens*. The six species are most prominent in that part of the field characterized by high basal area of lodgepole pine.

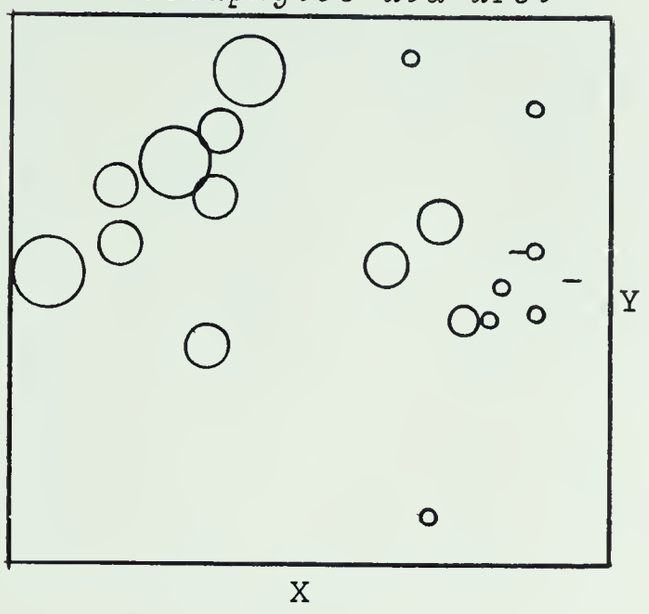
This visible correlation is further support for the positive association between herb and dwarf shrub stratum cover and lodgepole pine basal area first indicated by the multiple regression analysis (p. 175).

FIGURE 17. QUANTITATIVE PERFORMANCE OF SIX HERB OR DWARF SHRUB SPECIES ON THE 20-STAND ORDINATION

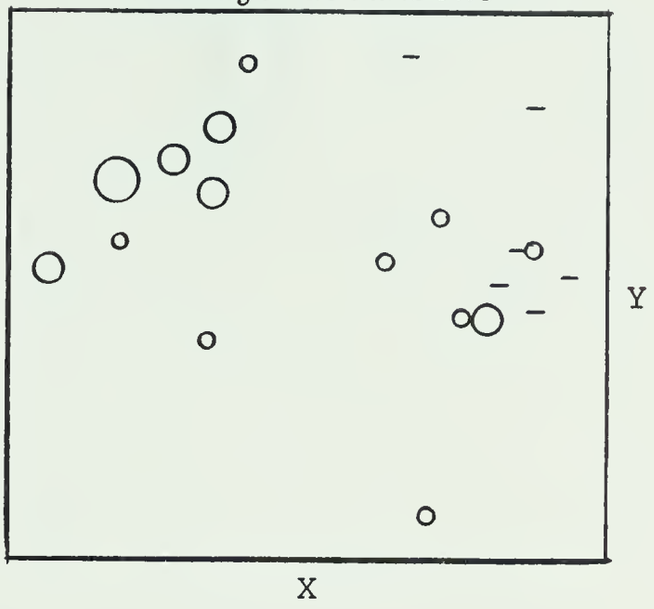
Progressively larger circles represent classes of 1 - 25, 26 - 50, 51 - 75 and 76 - 100% quadrat Frequencies.

No Frequency represented by a dash.

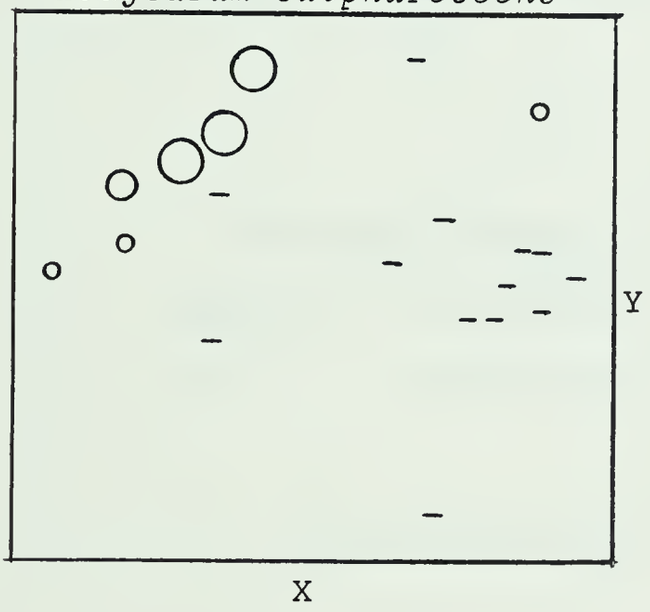
Arctostaphylos uva-ursi



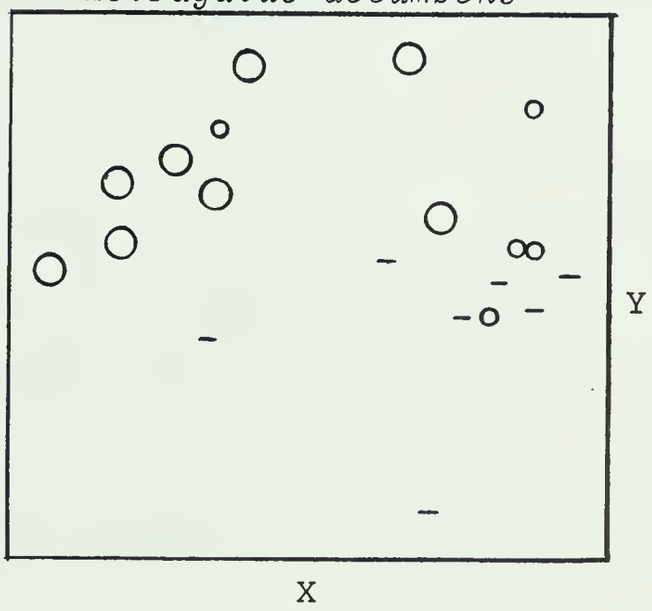
Solidago decumbens



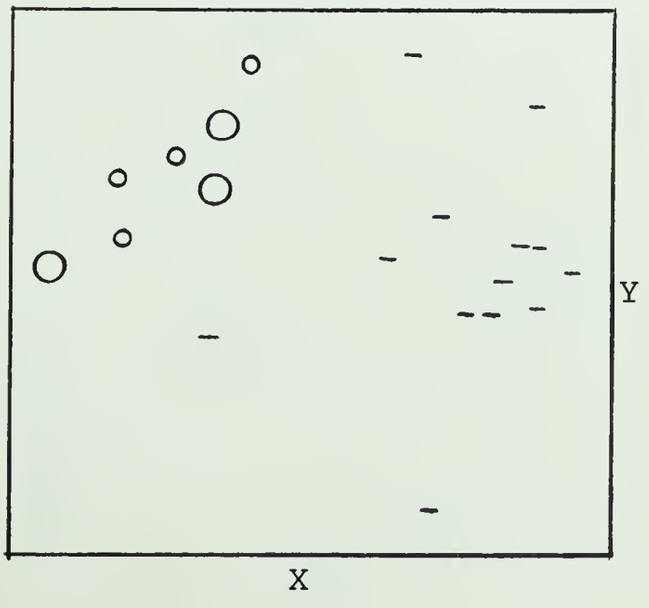
Hedysarum sulphurescens



Astragalus decumbens



Aster laevis



Festuca scabrella

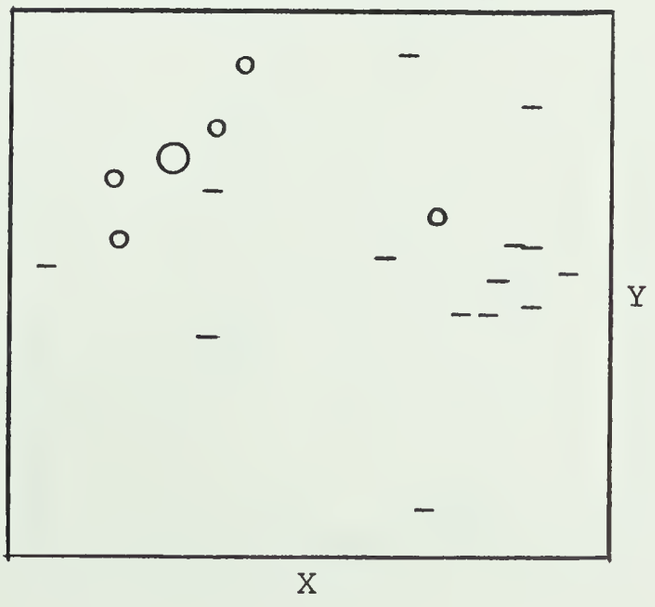
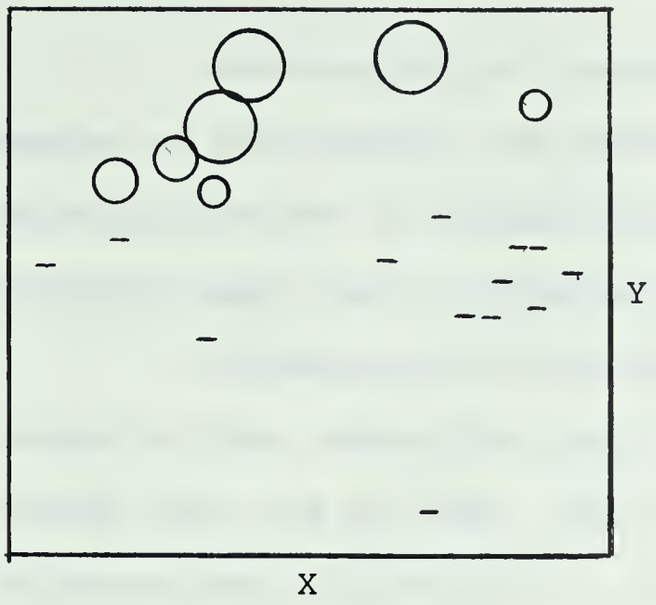


FIGURE 18. QUANTITATIVE PERFORMANCE OF THREE HERBS, TWO BRYOPHYTES AND ONE LICHEN ON THE 20-STAND ORDINATION

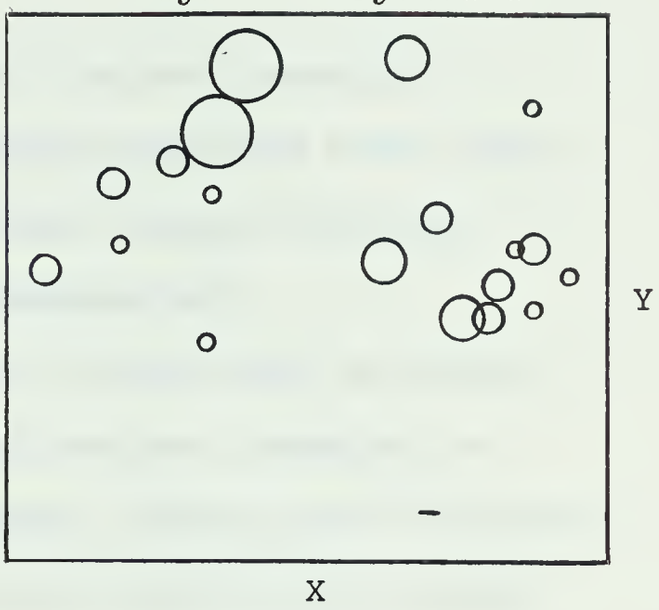
Progressively larger circles represent classes of 1 - 25, 26 - 50, 51 - 75 and 76 - 100% quadrat Frequencies.

No Frequency represented by a dash.

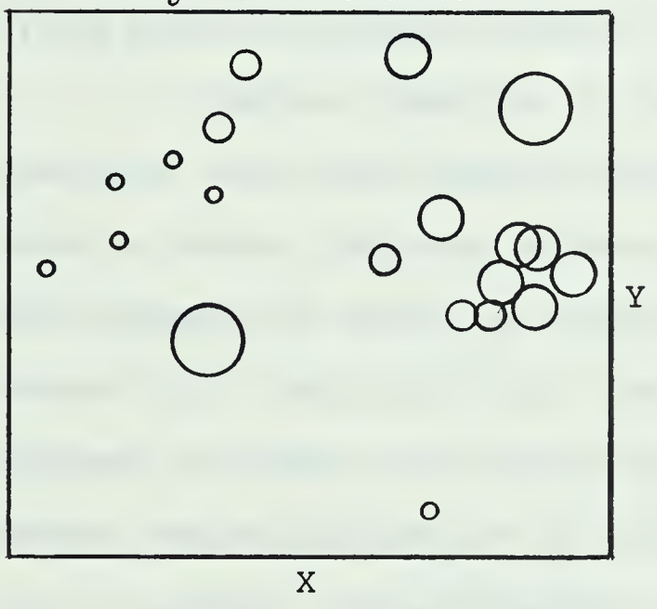
Calamagrostis rubescens



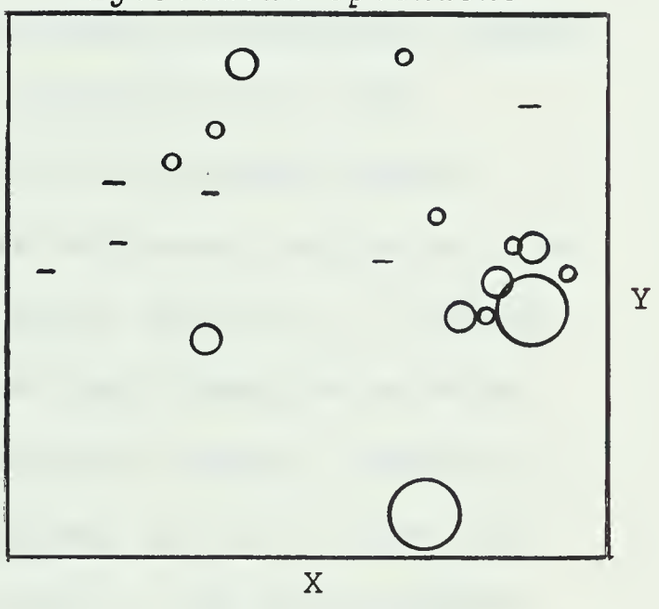
Fragaria virginiana



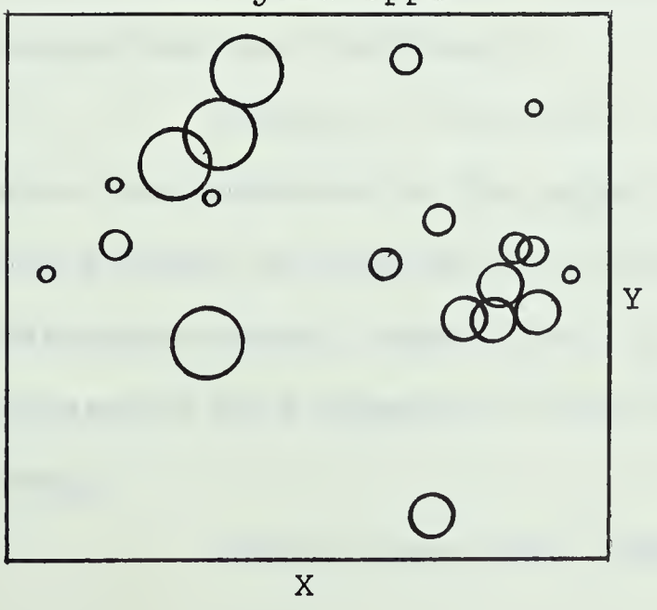
Elymus innovatus



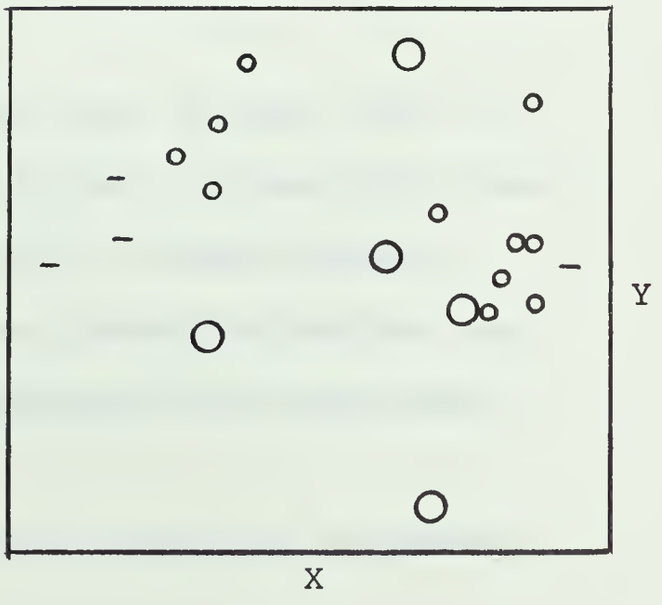
Hylocomium splendens



Peltigera spp.



Tortula ruralis



Arctostaphylos uva-ursi, the most prominent member of this group, was positively associated with lodgepole pine at the 1% probability level, using a 2x2 contingency table test on quadrat Presence data.

Calamagrostis rubescens is restricted to the top center of the ordination field and was most abundant in Stands 10B, 11B and 19B. This grass, together with *Hedysarum sulphurescens*, *Aster laevis*, *Festuca scabrella* and several other species of lesser prominence form a distinct species group which is almost entirely confined to the Banff stands.

Several species of low prominence but high Presence, are also characteristic of this Banff group: *Senecio canus*, *Agoseris glauca* and *Penstemon confertus*, the best example of which is *Senecio canus* (Fig. 16). Another *Senecio* (*S. cymbalarioides*) was the only vascular species present in Jasper and absent from Banff stands. However, before these species can be recognized as true "characteristic species" (Braun-Blanquet, 1932, p. 59) more comprehensive studies of their Presence or absence in surrounding ecosystems are necessary.

Fragaria virginiana, the most abundant forb, is also concentrated in the upper left part of the field, but its pattern of population size is not as well-defined. Although closely associated, it was therefore decided not to assign this species to the lodgepole pine associated group.

Elymus innovatus, the most prominent understory

species, is the only prominent herb to show a reversal of the trend towards maximum abundance in the left center or upper left parts of the ordination. It is most abundant in the right side of the field, in those stands with the highest tree canopy cover and basal area. This pattern suggests that *Elymus* is differently influenced by attributes of the tree canopy than are the major herbs and shrubs discussed above. Greater tolerance to factors limiting to most herbs is indicated, therefore giving this species a competitive advantage under well-developed Douglas fir canopies.

It is possible that the parallel drawn so far between the patterns of population size of most herbs and shrubs, and the attributes of the tree canopy is too simplified a picture, and that correlated environmental factors such as elevation and soil composition, may be more operative in causing the floristic discontinuity.

Other important herb and dwarf shrub species, including *Linnaea borealis*, *Aster conspicuus*, *Galium boreale* and *Lathyrus ochroleucus* showed no well-defined ordination patterns.

The forb:grass ratio (based on cover data) of all stands were plotted on the ordination field (Fig. 19). This ratio is of some use to the animal ecologist in determining the carrying capacity or grazing value of land and the species of ungulates that graze or browse there.

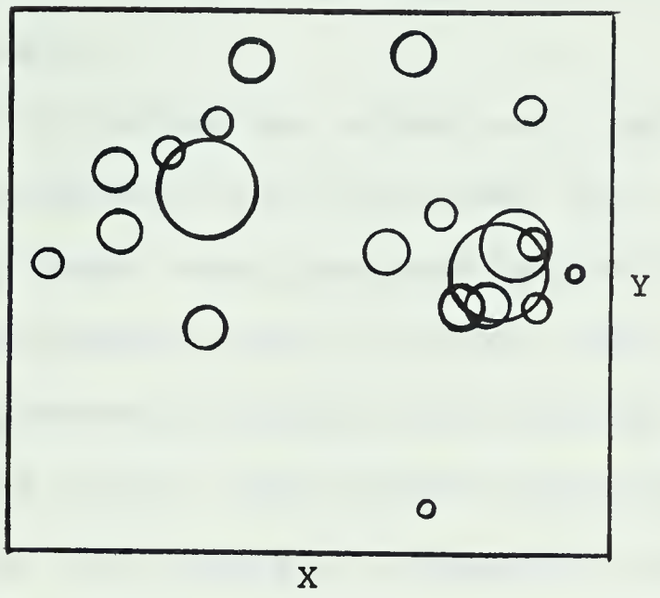
The ratio was first determined using the cover of

FIGURE 19. PATTERNS OF FORB/GRASS AND FORB + DWARF SHRUB/GRASS RATIOS ON THE 20-STAND ORDINATION

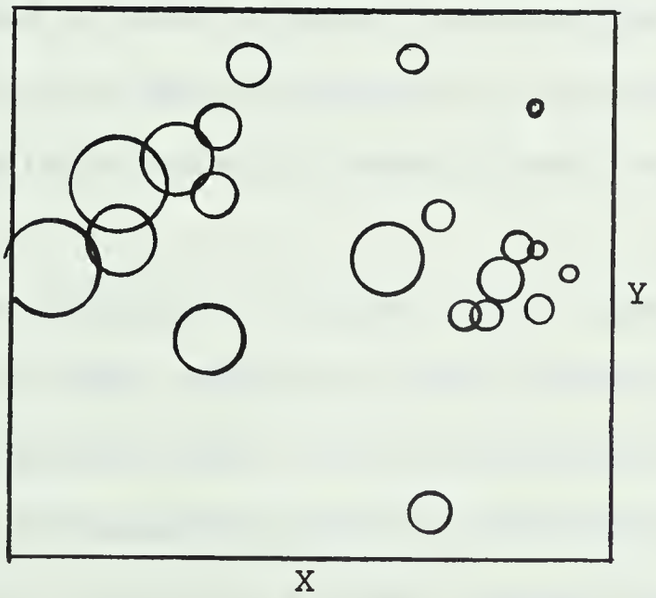
A. Forb/Grass Ratio: progressively larger circles represent ratio classes of less than 0.15, 0.15 - 0.30, 0.30 - 0.45, 0.45 - 0.60 and more than 0.60.

B. Forb + Dwarf Shrub/Grass Ratio: progressively larger circles represent ratio classes of less than 0.40, 0.40 - 0.80, 0.80 - 1.20, 1.20 - 1.60 and more than 1.60.

Forb/Grass Ratio



Forb + Dwarf Shrub/Grass Ratio



forbs and grasses only (Fig. 19A). The ordination shows no pattern; the relatively large cover values of *Elymus* and *Calamagrostis* result in very low ratios. Very low forb cover values introduce a disproportionately large error factor into these ratios.

Another set of ratios was calculated, including the cover of dwarf shrubs with the forb cover (Fig. 19B). Due to the relatively large cover provided by *Arctostaphylos uva-ursi*, and in some stands *Linnaea borealis*, the ratios became larger and a pronounced maximum was obtained in the upper left part of the field. This maximum approximates to that of the maximum of *Arctostaphylos* Frequency, and it is probable that this pattern is merely a result of the balance between the cover values of the three species largely contributing to the cover of this stratum (*Arctostaphylos uva-ursi*, *Elymus innovatus* and *Calamagrostis rubescens*). It is likely that periodicity will change these ratios considerably.

The high contribution of these three species to the total cover of the herb and dwarf shrub stratum, and their consequent dominating role in the forb:grass ratio may be a result of a favourable physical environment and/or the preferential grazing of other, potentially competitive species.

4. Bryophyte and lichen stratum

No total cover values for this stratum were plotted

as any patterns would merely reflect the distributions of the two or three predominant species (*Hylocomium splendens*, *Peltigera canina*, *Peltigera aphthosa*). Therefore, these species were plotted individually, their Frequencies being preferred to their cover values so as to obtain a wider range of values. The only species in this stratum that had high Frequency values (10% or more mean quadrat Frequency) and well-defined patterns on the ordination were *Hylocomium splendens*, *Tortula ruralis* and *Peltigera* spp. (Fig. 18).

Hylocomium, the most prominent constituent of feather moss carpets in this ecosystem, shows a maximum population size in the right center of the ordination field, in stands characterized by high total tree cover. This relationship was expected from its ability to tolerate low light intensities and its sensitivity to the extremes of temperature and moisture occurring in more exposed habitats.

Two members of the herb and dwarf shrub stratum, *Linnaea borealis* and *Pyrola secunda*, are strongly associated with *Hylocomium* at the 1% level of probability, using the 2x2 contingency table test. Apparently these two species can co-exist with feather mosses under micro-environmental conditions limiting to most other small vascular plants.

The *Peltigera* species group shows a poorly -defined bimodal pattern with maxima in the upper left and center right part of the field. The different habitat relations of the two major species found in this ecosystem, *Peltigera canina* and *P. aphthosa*, may be reflected in this

bimodal pattern.

Tortula ruralis is most abundant down the center of the ordination field, and is less common in the areas characterized by either

1) high tree canopy cover and basal area or
2) high Frequency of most herb and shrub species.

The only other variable that shows this type of pattern is available phosphorus at a depth of 10 inches. This association is somewhat reinforced by a strong positive correlation between available phosphorus in the top mineral horizon and the Frequency of *Tortula* ($r = +0.7664$). No hypothesis to relate these two variables can be proven with the limited data available, but it is probable that other environmental factors are causing the apparent association, rather than *Tortula* having a high phosphorus requirement.

5. Physical environmental variables on the ordination

Only six quantitative environmental variables show clearly-defined patterns of intensity (Fig. 20). They are elevation, field capacity at 10 inches, permanent wilting percentage at 10 inches, hydrogen ion concentration at 10 inches, maximum free lime in the mineral horizons and available phosphorus at 10 inches.

Elevation (uncorrected for latitude), shows a clear division between the higher Banff and lower Jasper parts of the ordination. Thus it is possible that unmeasured factors

FIGURE 20. PATTERNS OF SIGNIFICANT, QUANTITATIVE ENVIRONMENTAL VARIABLES ON THE 20-STAND ORDINATION

A. Mean Elevation: progressively larger circles represent classes of 3200 - 3700, 3700 - 4200, 4200 - 4700, 4700 - 5200 and 5200 - 5700 feet.

B. Field Capacity at 10 inches depth: progressively larger circles represent classes of less than 15, 15 - 20, 20 - 25, 25 - 30 and more than 30 percent.

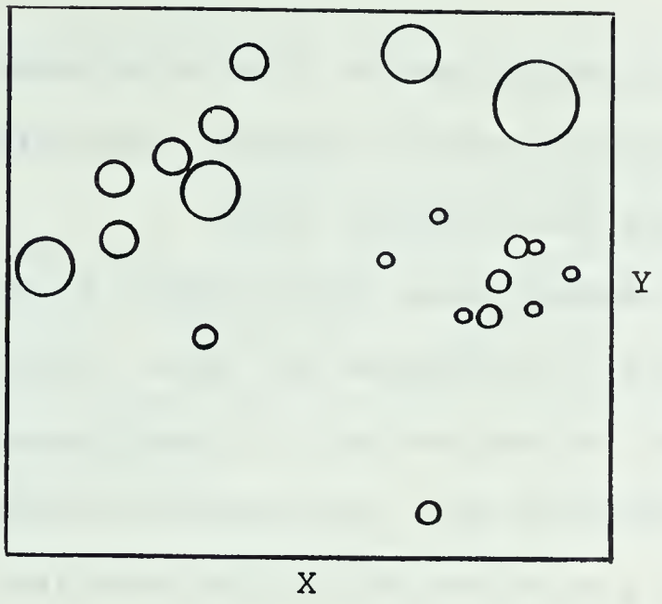
C. Permanent Wilting Percentage at 10 inches depth: progressively larger circles represent classes of less than 5, 5 - 10, 10 - 15, 15 - 20 and more than 20 percent.

D. Hydrogen Ion Concentration at 10 inches depth: progressively larger circles represent classes of less than 5 ($x10^{-8}$), 5 - 10, 10 - 25, 25 - 50 and more than 50 ($x10^{-8}$) moles per litre.

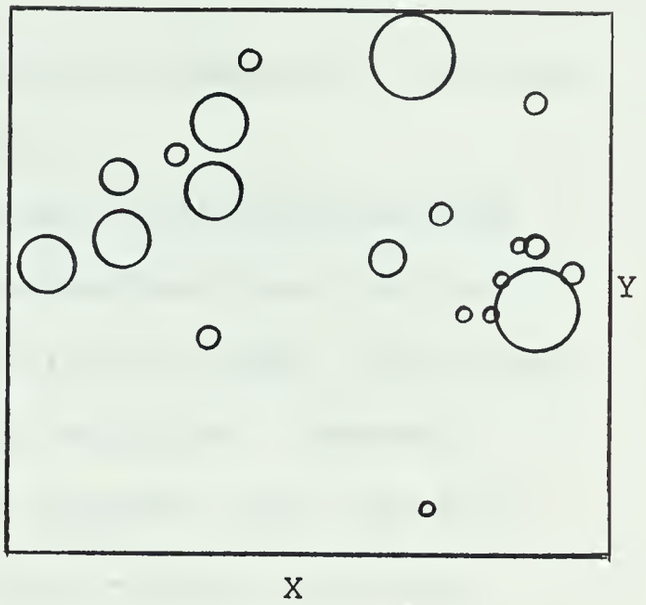
E. Free Lime; maximum in the mineral horizon: progressively larger circles represent low, medium, high and very high. No free lime present represented by a dash.

F. Available Phosphorus at 10 inches depth: progressively larger circles represent classes of less than 5, 5 - 10, 10 - 15, 15 - 20 and more than 20 pounds per acre.

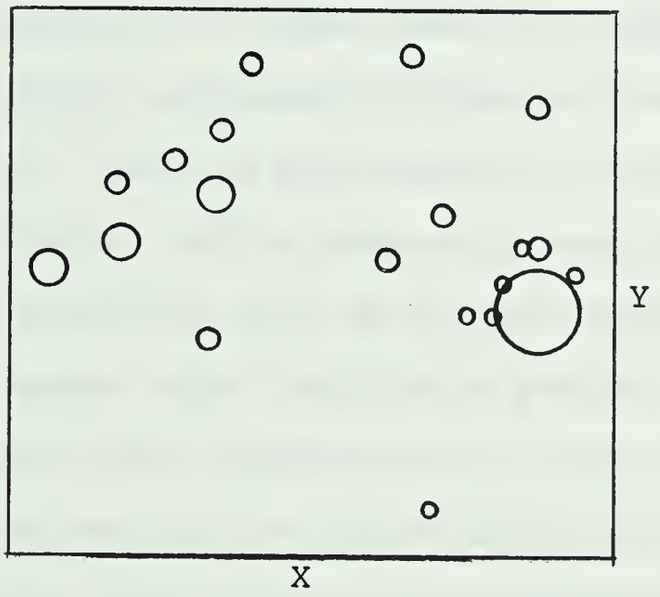
Mean Elevation



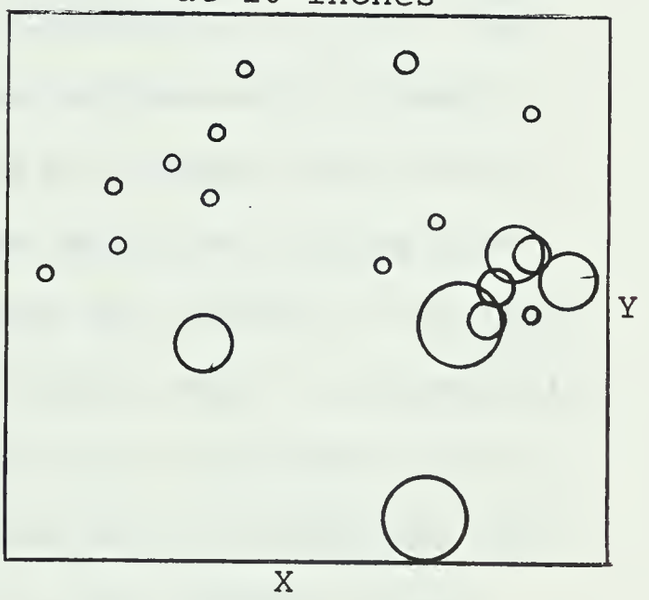
Field Capacity
at 10 inches



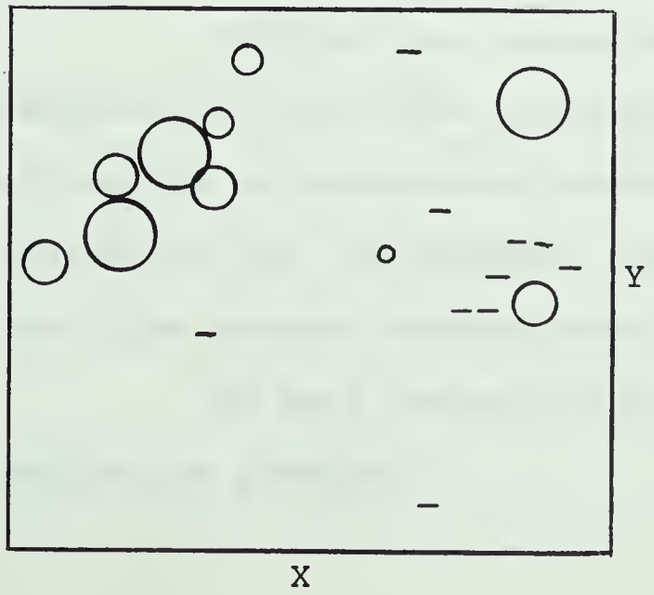
Permanent Wilting %
at 10 inches



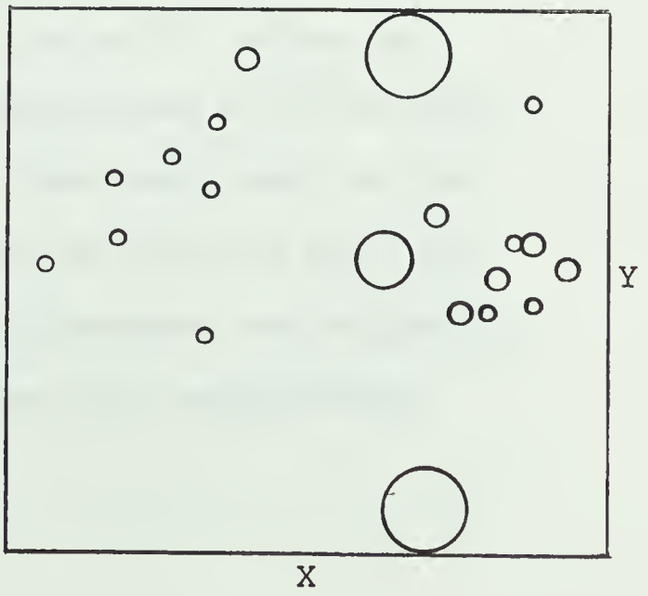
Hydrogen Ion Concentration
at 10 inches



Free Lime



Available Phosphorus
at 10 inches



correlated with elevation are partially responsible for the floristic trends of this ordination.

Field capacity and permanent wilting percentage at 10 inches depth were highest in the Banff part of the field, with the exception of Stand 12J at Jasper, which had exceptionally high values for both variables. However, water availability, the difference between these two soil characteristics did not show a clearly-defined pattern.

Precipitation at Banff, especially in the early spring, is higher than at Jasper (Chapter 3, p. 28). The higher permanent wilting percentage of the soil at Banff will require more moisture to make soil water available to plants, and so proportionately more water and spring precipitation will be needed to recover the losses of the late summer water deficiency period. In this way, it is possible that the higher precipitation, and higher permanent wilting percentage and field capacity of the soil at Banff may have the same effect on the vegetation as the somewhat lower values at Jasper.

Hydrogen ion concentration at 10 inches and maximum free lime show patterns associated with the type of bedrock or substratum present; the Banff part of the ordination has low hydrogen ion concentrations and high free lime content attributable to limestone and dolomite.

No soil texture variables give satisfactory ordination patterns.

Integration

It has been demonstrated that a clearly-defined floristic discontinuity exists between the Banff and Jasper areas. It has also been shown that at least six sets of environmental factors are associated with the discontinuity, including:

1) elevation
2) climate and relationship between evapotranspiration and precipitation
3) edaphic factors associated with soil water relations
4) edaphic factors associated with the lime content of the soil
5) the proportion of lodgepole pine in the canopy
6) structural attributes of the tree canopy.

These six sets of factors probably do not operate independently and evaluation of their relative influence cannot be deduced from the data available. However the combined effect of these six, probably together with other unknown factors, is a clear division between the producer levels of the Douglas fir ecosystems of the two National Parks. The possibility remains that this vegetational discontinuity is primarily a consequence of attributes of the tree canopy, which in turn may be a consequence of local

stand history.

It is notable that Stand 7B, the oldest stand at Banff, is older than four of the Jasper stands, and is in an intermediate position on the ordination field. Also two of the four younger stands at Jasper (3J and 16J) are in an intermediate position. This is additional support for the hypothesis that the discontinuity is mainly a function of stand history.

However, Stand 7B is also the highest elevation stand in Banff, suggesting that the highest part of the Douglas fir ecosystem at Banff is environmentally and floristically equivalent to the ecosystem at Jasper. Thus the index to compensate elevation for latitude (Hopkins, 1938) may be closer to 200 than 100 feet per 15 minutes of latitude in this region. This hypothesis would have to be supported by far more evidence than is available in this study.

It would be rash to categorically state that two well-defined ecosystems exist within the Douglas fir dominated vegetation of the study region, on the basis of these ordination results. This problem can only be solved with certainty when it is possible to completely separate the effects of stand history from those of environmental variables.

However, it has been demonstrated in this study that ordination is a useful method of detecting and describing floristic and vegetational discontinuities, and of showing the relations between environmental variables and

these biological attributes of the ecosystem.

X DISCUSSION AND CONCLUSIONS

The primary producer level of the mature phase of the Douglas fir ecosystem in Banff and Jasper National Parks is characterized by relatively few constant species. Only 15 vascular species of 140 listed have a Presence value in excess of 80%; these species are *Pseudotsuga menziesii* and *Pinus contorta* in the tree stratum, *Shepherdia canadensis*, *Rosa acicularis*, *Spiraea lucida* and *Juniperus communis* in the shrub stratum, and *Elymus innovatus*, *Arctostaphylos uva-ursi*, *Fragaria virginiana*, *Galium boreale*, *Aster conspicuus*, *Achillea millefolium*, *Solidago decumbens* and *Campanula rotundifolia* in the herb and dwarf shrub stratum.

Most vascular species have a limited within-stand distribution with only 12 having a mean quadrat Frequency in excess of 20%. These species are *Pseudotsuga menziesii* and *Pinus contorta* in the tree stratum, *Shepherdia canadensis*, *Rosa acicularis* and *Spiraea lucida* in the shrub stratum, and *Elymus innovatus*, *Arctostaphylos uva-ursi*, *Fragaria virginiana*, *Calamagrostis rubescens*, *Linnaea borealis*, *Aster conspicuus* and *Astragalus decumbens* in the herb and dwarf shrub stratum.

Douglas Fir

Douglas fir attains a maximum measured height of 140 feet and 44 inches DBH in Jasper and Banff National Parks.

The maximum recorded age at breast height was 367 years.

Douglas fir usually occurs on sandy-loam to loam soils derived from rocky, glacial till or outwash parent materials. Stands are situated on well-drained sites such as the top of ridges and the basal slopes of the mountains. Sites on slopes are usually south-facing in aspect and often subject to the maximum daily temperatures. These exposed ridges and basal slopes are not as subject to cold air drainage as the valley bottoms (Geiger, 1957, p. 204). It is therefore possible that Douglas fir populations of Banff and Jasper are excluded from the valley bottoms as much by intolerance of temperature minima there, as by summer moisture deficiencies, as suggested by Daubenmire (1943a). Another factor which seems operative in restricting fir to slopes and ridges is soil texture; valley bottoms tend to have finer, more compact soils than ridges and slopes. Douglas fir requires a well-aerated soil of not too fine a texture for seedling development (Isaac and Dimock, 1958), and so may well be excluded from areas of poorly-aerated clay-rich soils, more prevalent on the valley floodplains.

Fir has a deep-penetrating taproot and can develop under more xeric soil conditions than some of its associates, notably white spruce and aspen. On extremely xeric south-facing slopes it often becomes established in clumps of *Juniperus communis* where early stages of development are protected from browsing and extremes of temperature.

The distributional data of this research project

support the observations of Patten (1963) in the Madison Range of Montana, Parker (1952) in the Palouse Range of northern Idaho and Moss (1944) in southwestern Alberta; the Rocky Mountain variety of Douglas fir is usually confined to a narrow range of suitable sites, such as gravelly slopes and ridges towards the northern limits of its geographical range. More xeric aspects are occupied by sagebrush, grassland or ponderosa pine forest throughout the northern Rockies, and on less xeric aspects by species of the next highest vegetation zone such as Engelmann spruce and sub-alpine fir.

The younger stands tend to occur on more southerly-facing slopes (p. 165), suggesting the hypothesis that topographic-edaphic combinations corresponding to the potential habitats for optimum development of Douglas fir are gradually changing as the climate becomes slightly more mesic. Locations on south-facing slopes previously too xeric for fir seem to have become more mesic.

This apparent trend is in agreement with the observations of Hansen (1948) on post-glacial forest succession in Glacier National Park and also Patten (1963) in the Madison Range of Montana, as follows. The principal pioneer of de-glaciated terrain was lodgepole pine because of its early seed-bearing age and its aggressiveness on sterile mineral soil in the absence of competition. Douglas fir and ponderosa pine, two species better able to tolerate xeric environments, became prominent during the post-Glacial

Xerothermic Maximum (approximately 4000 - 8000 years ago). In the last 4000 years, the climate has become cooler and more moist, resulting in the expansion of more mesophytic species such as white and Engelmann spruce and sub-alpine fir, so that Douglas fir has become progressively more restricted to the more xeric habitats by competitive exclusion.

Multiple regression analysis has indicated that, of those factors studied, slope aspect, available potassium, available phosphorus and stand age seem most influential in tree stratum development. A strong positive correlation between attributes of the tree stratum and the available potassium level in the mineral soil indicates that this nutrient is a major factor in limiting the carrying capacity of the primary producer level of this ecosystem.

Other Tree Species

The only common associate of fir in the canopy of the Douglas fir ecosystem at Banff and Jasper is lodgepole pine. It has been found in this study that the older and more mature the stand, the lower is the proportion of pine in the tree stratum (p. 167). Pine is usually considered a seral species whose distribution and abundance is increased by fire disturbance (Horton, 1956). The extensive fires that have occurred in the Banff and Jasper region have produced large areas of uniformly-aged lodgepole pine, but this species rarely reproduces successfully under a closed canopy

(Horton, 1956). Therefore, it is likely that pine naturally reproduces in Douglas fir forest only when an opening occurs in the canopy, conditions also favouring the development of Douglas fir, aspen, white spruce and most understory species. The very low, observed reproduction of pine in Douglas fir stands is undoubtedly due in part to the National Parks policy of fire prevention, together with competitive exclusion by reproduction of other species.

The Presence and population size of lodgepole pine in a stand is strongly correlated with, and probably very influential on the floristic composition of the stand. On the two-dimensional ordination field, the area of maximum pine population size coincides with the area of maximum cover in the herb and dwarf shrub stratum. In multiple regression, the independent variable of lodgepole pine basal area appears very prominently in most of the equations pertaining to the prominence of major species in the herb and dwarf shrub stratum and to the equation of the total cover of this stratum.

A high proportion of pine is usually associated with a comparatively low total tree cover. The light requirements of pine needles are such that the living crowns of pine are often very shallow and diffuse. Consequently light and moisture conditions are more favourable to understory development, especially the herb and dwarf shrub stratum. The shrub and terrestrial bryophyte and lichen strata are not as influenced by the proportion of pine in

the stratum; the variable lodgepole pine basal area, does not appear prominently in the regression equations for the cover of these strata. The simple correlation coefficient between light intensity and lodgepole pine basal area was not significantly positive at the 5% level ($r = +0.1496$), as no attempt was made to compensate for the variation in total basal area.

Aspen may be the pioneer species on burned-over areas in the montane zone, if fires are not too severe, by proliferation of root suckers (Horton, 1956). However, aspen is far less common than pine on sites suitable for Douglas fir, due perhaps to its requirement for finer -textured soils of greater moisture-holding capacity. Therefore, in fir stands, aspen occurs in gullies or towards the base of slopes where the moisture content of the soil is likely to be more favourable and the soil texture finer (Daubenmire, 1943a).

Of the tree associates of Douglas fir in Banff and Jasper, only white spruce is more tolerant of shade (Baker, 1949); aspen, lodgepole pine and paper birch are less tolerant. White spruce is more sensitive to exposure and occurs more frequently on the more mesic, north-facing slopes and in moist gullies than does fir (Moss, 1944); it appears to require more soil moisture and snow cover for successful establishment.

When competing in habitats suitable for both, the spruce should eventually succeed the fir and form the

climax forest. Therefore, Douglas fir can only be considered climax in those areas of the Alberta montane zone which are less suitable for the development of spruce. Thus the Douglas fir ecosystem may be regarded as a topographic climax type and not the "prevailing climax" (Whittaker, 1953, p. 59) of normal sites in the main valleys of Banff and Jasper National Parks. In Stand 12J (and perhaps in Stand 16J) white spruce appears to be succeeding fir under more mesic environmental conditions than is normal for Douglas fir stands; it is suspected that the stand is supplied with abundant ground water (Dr. G.H. La Roi, Department of Botany, University of Alberta; personal communication). In most stands, however, spruce is either absent or restricted to moist hollows or gullies, so there is little evidence to believe that spruce is generally succeeding fir in any but a few ecotonal areas.

Maturation Cycle

A main objective of this study was to describe the mature phase of the Douglas fir ecosystem; therefore younger stages remain to be investigated. Selection of stands from aerial photographs also created a bias towards the older stands.

A regular maturation cycle may be operative in the development of Douglas fir forests, to which pine and aspen may contribute only when this cycle is disturbed, especially

by fire.

As the Douglas fir forest matures, the canopy becomes increasingly irregular in height (p. 77). Reproductive stages of all tree species are scattered and sparse because none of them, with the possible exception of white spruce, can develop successfully under a heavy, closed tree canopy. As the canopy matures, the density decreases due to increasing competitive effects, and eventually openings appear due to natural mortality.

These openings then support a large number of shrub and herb species as well as early reproductive stages of fir and possibly pine, spruce and aspen. As a result of the development of these openings or "Gap Phases" (Watt, 1947), patches of trees of different size, age and often species develop and a contagious distribution is the inevitable result.

As these patches increase in age, competitive thinning occurs and the local forest pattern becomes more and more like that of the mature phase, where dispersion is more random. This especially applies to the shade intolerant pine; it has been shown that the larger pine tend to be widely spaced, unlike the young trees which are invariably clumped (p. 106). The frequent fires that have occurred in the main valleys of Banff and Jasper have interfered with this cycle. A crown fire will kill all trees present and the burn area will eventually become a uniform-aged forest of pine, fir or possibly aspen de-

pending on the species present previous to the fire, the local environment and the fire's severity. For example, Stand 8B is a uniform stand of fir and pine in which the ages of nearly all trees studied were between 50 and 75 years. It can be hypothesized that a crown fire occurred there in about 1890.

If the fire is not too severe, many of the older fir will survive due to their thick fire-resistant bark, and a two-aged stand will result. For example, Stand 13J contains three distinct age-groups of trees, including a few old relic fir mostly over 300 years, a larger number of fir with ages ranging from 163 - 178 years, and an even larger number of young fir and pine aged between 46 and 58 years. Again it can be hypothesized that major disturbances, probably fire, occurred approximately 60 and 180 years ago.

If all trees are killed by fire, it is unlikely that fir will play a role in the early stages of succession thereafter, unless seed is dispersed into the area from outside. Instead a "semi-permanent" forest of aspen or pine commonly develops (Daubenmire, 1943a). The occurrence of isolated old relic fir with or without patches of associated reproduction, in young or medium-aged pine or sometimes aspen forest, can be accounted for by this hypothesis.

The very uniform age of many of the Douglas fir stands at Banff (p. 78) suggests that fires burned over much of Bow Valley in the last century. Five stands appear

to have originated following severe fires that occurred between 1880 - 1890, the years of railroad development and early settlement (p. 36). Three other Banff stands also appear to have suffered fire damage around 1880 - 1890 but older fir trees persisted and two or several-aged stands have resulted.

In contrast, no clear age-classes related to fire history are apparent from ring-counts of trees at Jasper. It must be concluded that fires there were less widespread and less intense. The years of railroad construction in Jasper (1910 - 1912; p. 37) are not correlated with 50 year-old fire stands of fir.

There is a reasonable expectancy of at least one fire during the life-span of a Douglas fir forest. Therefore lodgepole pine can be considered as a part of the Douglas fir maturation cycle.

Subordinate Vegetation

Over 50% of the ground surface is barren of vegetation due to factors limiting to the development of the understory strata such as the reduction of light intensity and moisture by the tree canopy, as well as the grazing and browsing of animals.

Multiple regression analyses have shown that the understory is highly correlated with attributes of the tree stratum, to a lesser extent with topography and very

little with edaphic factors.

The limitation to development of the understory strata imposed by the fir canopy is undoubtedly one of the causes of the low tree reproduction in most stands, although other factors of local importance, such as heavy browsing and trampling by ungulates, are probably important as well.

Multiple regression analysis has indicated that the sampled environmental factors having most influence on the structure of the shrub stratum are the total basal area and density of the tree stratum, and slope angle (p. 168). The influence of slope angle may indirectly result from the lower tree density, normally found on steeper slopes, allowing a greater cover of xerophytic, light-demanding shrubs such as *Juniperus communis* and *J. horizontalis*.

The four most prominent shrubs are *Shepherdia canadensis*, *Rosa acicularis*, *Spiraea lucida* and *Juniperus communis*. They form a two-layered stratum with *Shepherdia* at a height of about 2½ feet, and all the other shrubs except *Salix* at 6 - 15 inches. In their response to the environment provided by the tree canopy they form a series from *Juniperus communis*, the most limited by shade and therefore most restricted in distribution, through *Spiraea* and *Shepherdia* to *Rosa acicularis* which has a higher tolerance to microenvironmental variation (high quadrat Frequency but a relatively low cover).

Cover of the herb and dwarf shrub stratum was positively correlated with free lime content of the soil; bacterial breakdown of organic matter will be limited in the more acid soils, thus adversely affecting the cycling of nutrients in these nutrient poor soils, and indirectly, the productivity of the understory. The greatest development of this stratum is therefore at Banff where a combination of favourable factors is found: high free lime content, low canopy cover, high proportion of pine and high availability of moisture in early summer.

The most prominent species in the herb and dwarf shrub stratum are: *Arctostaphylos uva-ursi*, *Elymus innovatus*, *Calamagrostis rubescens*, *Astragalus decumbens*, *Fragaria virginiana*, *Aster conspicuus*, *Linnaea borealis* and *Hedysarum sulphurescens*.

The terrestrial bryophyte stratum is best developed on protected north-facing slopes and under old, mature tree canopies where the limitations of a heavy canopy cover exclude most herbs and shrubs. The most prominent species are *Hylocomium splendens*, *Abietinella abietina*, *Tortula ruralis*, *Drepanocladus uncinatus* and *Hypnum revolutum*. *Tortula* is prominent on dry, shaded soils and litter under dense fir canopies, and is associated with soils relatively rich in available potassium.

Terrestrial lichens are not abundant, the only prominent species being *Peltigera aphthosa* in moist shady habitats, *Peltigera canina* var. *rufescens* on dry, exposed

south-facing slopes, and many unidentified species of *Cladonia*.

The composition and structure of the understory will tend to change with the maturation cycle because relatively few species can survive beneath a closed fir canopy. The grass *Elymus innovatus* and the feather moss *Hylocomium splendens* can grow and reproduce in this habitat, whereas most of the species associated with them in earlier phases of the cycle cannot. Thus *Elymus* and *Hylocomium* tend to be relatively more abundant in stands with higher tree cover (pp. 205 and 208) as a consequence of environmental selection and competitive exclusion.

Relatively few major species in this ecosystem are equally prominent in both Banff and Jasper. These are *Shepherdia canadensis*, *Aster conspicuus*, *Galium boreale*, *Achillea millefolium* and the *Peltigera* species. Species more prominent at Banff are *Pinus contorta*, *Spiraea lucida*, *Juniperus communis*, *Arctostaphylos uva-ursi*, *Fragaria virginiana* and *Astragalus decumbens*. A number of prominent species are almost entirely restricted to Banff stands, namely *Juniperus horizontalis*, *Calamagrostis rubescens*, *Hedysarum sulphurescens*, *Aster laevis* and *Festuca scabrella*. It is suspected, however, that at least some of these occur prominently in Jasper but in different ecosystems; *Calamagrostis* has been reported as abundant in stands of aspen and lodgepole pine in the Snake Indian River area of northern Jasper (Dr. G.H. La Roi, Department of Botany, University of

Alberta; personal communication), so that its exclusion from the eleven stands at Jasper is probably due not to its geographical distribution, but to its exclusion from mature, closed-canopy forest.

The only major species to be more prominent at Jasper are *Rosa acicularis* and *Elymus innovatus*, both prominent species of northern boreal forests.

Classification

Because there are significant differences in the floristic composition and in certain environmental factors between the Douglas fir stands of Banff and Jasper, it seems reasonable to distinguish two different ecosystem types or "associations" (in the sense used by Daubenmire, 1952) within the primary producer level of the Douglas fir vegetation.

Most of the stands at Jasper are characterized by the dominance of *Elymus innovatus* in the understory. Since the shrub, lichen and bryophyte strata are relatively unimportant, it seems reasonable to name an "association" for the Jasper area composed of two "unions" (Daubenmire, 1952), the *Pseudotsuga menziesii/Elymus innovatus* association. This association is characterized also by the prominence of *Shepherdia canadensis* and *Rosa acicularis* in a poorly-developed shrub stratum, *Linnaea borealis* and *Arctostaphylos uva-ursi* in the herb and dwarf shrub stratum,

and *Hylocomium splendens* and *Abietinella abietina* in the feather moss carpet.

At Banff, *Elymus innovatus* is usually far less prominent than either *Arctostaphylos uva-ursi* or *Calamagrostis rubescens* in the herb and dwarf shrub stratum. The shrub and terrestrial bryophyte and lichen strata are relatively unimportant, although the first is better developed in Banff than Jasper. The Banff area can thus be classified as a second two-union association, the *Pseudotsuga menziesii/Arctostaphylos uva-ursi - Calamagrostis rubescens* association. This association is characterized by the additional prominence of *Juniperus communis*, *J. horizontalis*, *Spiraea lucida*, *Shepherdia canadensis* and *Rosa acicularis* in the shrub stratum, a great number of species including *Fragaria virginiana*, *Astragalus decumbens* and *Hedysarum sulphurescens* in the herb and dwarf shrub stratum and a very poorly developed terrestrial bryophyte and lichen stratum.

It is notable that, of the two major species in the herb and dwarf shrub stratum of the *Pseudotsuga/Arctostaphylos - Calamagrostis* association, *Arctostaphylos* is more prominent in those stands with relatively high free lime content in the soil and therefore an alkaline pH value, whereas *Calamagrostis* is more prominent in those stands with correspondingly low values for these factors.

Stand 7B at Banff appears to resemble the *Pseudotsuga/Elymus* association at Jasper rather than the

other stands at Banff; it is also the highest in elevation of the Banff stands.

It must be emphasized that these two associations could represent different phases in the maturation cycle of Douglas fir forest, as follows.

The *Pseudotsuga/Elymus* association represents the old closed-canopy phase of the maturation cycle, with very sparse understory vegetation. The *Pseudotsuga/Arctostaphylos - Calamagrostis* association is far more variable, often possessing a discontinuous canopy of Douglas fir and lodgepole pine, and possibly representing an earlier phase in the maturation cycle.

It is also possible that the floristic discontinuity between Banff and Jasper, represented by the two associations, is partly a result of factors other than stand history. Therefore TWO maturation cycles, similar in structure, but differing in the species composition and population sizes in the understory strata, may be operative in Banff and Jasper. Floristic differences between Banff and Jasper stands could then be a consequence of environmental factors influencing the distribution and the competitive ability of individual understory species, as well as the bulk of the stands representing different phases in structurally similar maturation cycles.

A number of environmental and historical factors may by their influence account for differences in the distribution and abundance of understory species at Banff and

Jasper. Some have been previously listed in the chapter on Ordination (p. 212). Their contrasts may be summarized as follows.

Banff	Jasper
Soils alkaline to neutral, with free lime usually present.	Soils acid to neutral, with free lime usually absent.
Higher elevation (4600 - 5520 feet) but lower latitude (51°8' to 51°14' North).	Lower elevation (3390 - 4000 feet) but higher latitude (52°48½' to 53° 9½' North).
Younger tree stratum with low canopy cover and lodgepole pine prominent.	Older, more mature tree stratum with high canopy cover and little lodgepole pine.
Higher field capacity and permanent wilting percentage values in the soil.	Lower field capacity and permanent wilting percentages.
Higher precipitation, especially in spring as well as less water deficiency in late summer.	Lower precipitation in spring and greater water deficiency in late summer.

There are several reasons for assuming that free lime content and acidity of the soil are of relatively minor importance:

a) Stand 7B, with a high free lime content, is floristically more similar to Jasper than to Banff (p. 213);

b) Stand 10B with no free lime and an atypical C horizon is floristically a typical example of the *Pseudotsuga/Arctostaphylos - Calamagrostis* association;

c) The hydrogen ion concentration variable played no prominent part in any of the multiple regression equations pertaining to the tree stratum.

The slightly higher field capacity and permanent wilting percentage values at Banff may be compensated for by the higher precipitation there, especially in late winter and spring, resulting in soil moisture conditions similar to those of Jasper stands. Water availability does not appear prominently in the multiple regression equations pertaining to the tree stratum; therefore moisture relations of the soil also seem to have relatively minor influence on the species composition and population size differences between Banff and Jasper.

Meteorological data suggest that the climatic differences between the two areas are not of major importance. The somewhat longer period of moisture deficiency, higher summer temperatures and lower precipitation of Jasper will no doubt influence the distribution of a number of species near their limits of tolerance for these factors. However, most of the prominent species have concluded vegetative growth and flowered before the moisture de-

ficiency becomes operative.

The similarity of Stand 7B to the Jasper stands, together with its higher elevation than the rest of the Banff stands, indicates that the two areas may not be elevationally and zonally equivalent. However, Stand 7B has other atypical features; it is the oldest stand at Banff and has very little pine in the tree stratum. These latter features can equally account for this stand's similarity to those of Jasper, and the question of whether or not Banff and Jasper areas are elevationally equivalent must be left in abeyance for lack of evidence.

The floristic discontinuity between Banff and Jasper is based solely on the composition and abundance of species in the shrub stratum and the herb and dwarf shrub stratum. Therefore there is high significance in the fact that attributes of the tree stratum such as effective stand age, total tree cover and basal area give such clearly-defined patterns on the ordination field and also are the most influential variables appearing in the multiple regression equations of the understory. This is strong evidence of a close dependence between floristic composition and structure of the understory strata and the maturity of the tree canopy.

It is therefore likely that the floristic discontinuity between Banff and Jasper is primarily a consequence of stand history, although climatic and edaphic differences probably have some influence in individual

species distributions and population sizes.

Douglas Fir in Other Parts of the Rocky Mountains

The information obtained from one stand at Waterton (21W) is inadequate for detailed comparison purposes. However, this stand differs so greatly from those of Banff and Jasper, both in composition of the vegetation and in macroclimate, that the Douglas fir ecosystem at Waterton cannot be considered as a part of the Douglas fir ecosystem at Banff and Jasper. Further studies are necessary to determine just how typical this stand at Waterton is of the Douglas fir forests in southwestern Alberta.

It is informative to compare the primary producer level of the mature phase of this Douglas fir ecosystem with other Douglas fir ecosystems in the northern Rocky Mountains.

Geographically, the closest detailed study of this nature was carried out by McLean and Holland (1958) in the Upper Columbia Valley of British Columbia. They named three associations in the Douglas fir zone of this valley. The Douglas fir/pinegrass (*Pseudotsuga menziesii /Calamagrostis rubescens*) association was named as climax on grey-wooded soils over most of this zone. Many of the "principal" species of this association are prominent or

common in Banff and Jasper Douglas fir forest: *Shepherdia canadensis, Calamagrostis rubescens, Arctostaphylos uva-ursi, Linnaea borealis, Aster conspicuus, Lathyrus ochroleucus, Vicia americana, Astragalus decumbens, Arnica cordifolia, Pyrola secunda, Agropyron spicatum* and *Agropyron dasystachyum.* Lodgepole pine and aspen were named as important seral species occupying large areas after fire or logging. This Douglas fir /pinegrass association bears a very close resemblance to both Banff and Jasper forests, the only prominent species missing from the Douglas fir/pinegrass association being *Elymus innovatus* and *Juniperus communis*.

Tisdale and McLean (1957) considered the *Pseudotsuga /Calamagrostis* association as climax over a large part of the Douglas fir zone in southern British Columbia. The dry climate of this zone (in the rain shadow of the Cascade Range) is similar to that at Banff and Jasper, and fir reaches about the same maximum size (115 feet high and 40 inches DBH) in both regions. Tisdale and McLean name the following as "principal" species: *Pseudotsuga menziesii, Pinus contorta, Populus tremuloides, Rosa gymnocarpa* Nutt., *Shepherdia canadensis, Spiraea lucida, Amelanchier alnifolia, Arctostaphylos uva-ursi, Linnaea borealis, Vaccinium caespitosum, Calamagrostis rubescens, Fragaria virginiana, Carex richardsonii, Aster conspicuus, Arnica cordifolia, Goodyera oblongifolia, Mahonia repens, Lathyrus ochroleucus, Vicia americana, Achillea millefolium, Astragalus decumbens, Hieracium albiflorum, Hieracium umbellatum* L., *Viola adunca,*

Pyrola secunda and *Taraxacum officionale*.

It is notable that 22 of these 26 species are also prominent or common at Banff and Jasper. Again, a notable difference is the absence of *Elymus innovatus* and *Juniperus communis*.

Brayshaw (1965) named four major associations in the Douglas fir zone of British Columbia:

1) "*Pseudotsuga menziesii* - *Pinus ponderosa* - *Arctostaphylos uva-ursi* association as climax or grazing disclimax of (2) from 2000 - 4000 feet on gravelly soils or stony tills;
2) *Pseudotsuga* - *Arctostaphylos* - *Calamagrostis rubescens* association as climatic climax from 2500 - 4000 feet on coarse to medium-textured soils;
3) *Pseudotsuga* - *Calamagrostis* association as climax from 2800 - 4300 feet on medium to fine-textured soils;
4) *Pseudotsuga* - *Symphoricarpos albus* association as a topographic climax at 1500 - 3000 feet in shallow draws, ravines and moist slopes."

The dependence of the first three of these associations on soil texture has not been paralleled by observations at Banff and Jasper, for *Calamagrostis* and *Arctostaphylos* show no significant correlation with soil texture. Instead, their distributions are apparently more affected by soil

acidity, a direct reflection of the composition of the bedrock or glacial drift.

The lists of "characteristic associates" of the four associations described by Brayshaw (1965) all bear some resemblance to the species lists from Banff and Jasper. For example, prominent or common species at Banff and Jasper also named by Brayshaw are as follows:

1) for the *Pseudotsuga - Pinus ponderosa - Arctostaphylos* association, *Juniperus communis*, *Amelanchier alnifolia*, *Fragaria virginiana*, *Carex concinnoides*, *Antennaria neglecta* and *Allium cernuum*;
2) for the *Pseudotsuga - Arctostaphylos - Calamagrostis* association, *Fragaria virginiana*, *Allium cernuum*, *Carex concinnoides* and *Astragalus decumbens*;
3) for the *Pseudotsuga - Calamagrostis* association, *Pinus contorta*, *Populus tremuloides*, *Aster conspicuus*, *Antennaria rosea* and *Arnica cordifolia*;
4) for the *Pseudotsuga - Symphoricarpos* association, *Populus tremuloides*, *Spiraea lucida* and *Clematis verticellaris*.

Of the list of 33 "characteristic associates" named by Brayshaw, 15 are prominent at Banff and Jasper, although no single one of these four associations bears a close floristic

resemblance to those described in this study.

The only prominent species that are completely missing from these lists of Brayshaw, McLean and Holland and Tisdale and McLean are *Elymus innovatus*, *Rosa acicularis* and *Picea glauca*, all of which are generally considered to be northern species of the boreal forest. It is notable that *Elymus* and *Rosa acicularis* are more prominent at Jasper than at Banff.

It is evident that the Douglas fir areas of Banff and Jasper are very similar floristically to the Douglas fir zone of southern British Columbia, and it is therefore possible to look upon them as eastern extensions of this zone through passes in the Rocky Mountains.

Patten (1963) studied the Douglas fir communities of the Madison Range of Montana. He found fir occurring as a physio-edaphic climax species on microenvironmentally favourable sites at elevations above those at which it is normally found at that latitude. The ground cover was very similar to that of the drier lodgepole pine forest of the same region. Of the 16 vascular species named by Patten as important associates of Douglas fir, 9 are also prominent or common at Banff or Jasper: *Shepherdia canadensis*, *Juniperus communis*, *Symphoricarpos albus*, *Rosa acicularis*, *Arctostaphylos uva-ursi*, *Linnaea borealis*, *Calamagrostis rubescens*, *Aster conspicuus* and *Arnica cordifolia*. This species list closely resembles the *Pseudotsuga/Arctostaphylos*

- *Calamagrostis* association of Banff, notable missing species being *Spiraea lucida*, *Hedysarum sulphurescens*, *Astragalus decumbens* and *Elymus innovatus*.

Patten (1963) stated that Douglas fir probably covered more of the area formerly than it does now, that it has retreated onto steep dry slopes with shallow rocky soils that could compensate for the cooling climate after the xerothermic period (4000 - 8000 years ago). Patten also stated that there is evidence of forest advance into sage-brush openings, indicating that the forested areas are gradually restocking the areas lost during the xerothermic period.

Observations in Banff and Jasper concerning the younger stands of fir being situated on more south-facing slopes are in agreement with this hypothesis.

Man's Influence

There has been and continues to be considerable influence of human and other animal populations on the primary producer level of the Douglas fir ecosystem at Banff and Jasper.

For many years prior to the early development of the parks, until the implementation of a fire control policy, the incidence of uncontrolled forest fires was considerable. During this period much of the climax forest was replaced by aspen and lodgepole pine forest, or by shrub and grassland,

and the potential browsing and grazing areas for ungulates was increased. Assisted by man's restocking of elk, the populations of ungulates increased until in the 1940's critical overstocking became apparent. Then steps were taken to keep the animal populations, especially elk, in check by annual harvesting. With continued fire control the forested areas of the main valleys will inevitably return to climax white spruce and Douglas fir and further reduce the area of suitable browsing and grazing habitat for the ungulate populations.

At the present time, the preferred shrub species such as *Amelanchier alnifolia* and *Spiraea lucida* together with *Symphoricarpos albus* (of questionable significance as browse), are browsed down to a height of 6 - 12 inches in many stands. This height may possibly correspond to the depth of winter snow. *Rosa acicularis* and *Rosa woodsii* appear to be of intermediate preference, and *Shepherdia canadensis*, *Juniperus communis* and *J. horizontalis* appear to be relatively little browsed. It is expected that the shrub strata of many forested areas in the main valley will retain an impoverished appearance for a long time, unless consumer activity declines markedly.

Unfortunately much of the Douglas fir vegetation of Banff and Jasper is situated close to townsites, on well drained, south-facing or level locations that are attractive for recreational and accommodational development. Any further development of such vegetation in the main valley

areas would make serious inroads into the remaining Douglas fir forests of the two parks, and should therefore be discouraged or directed elsewhere.

XI SUMMARY

1. The objectives of this study were to:
   1) describe the floristic composition, vegetation structure and the physical habitats of the mature phase of the Douglas fir ecosystem in Banff and Jasper National Parks, Alberta;
   2) to determine the major physical environmental factors operative on the primary producer level of this ecosystem.

2. Studies of aerial photographs, followed by a preliminary survey, resulted in the compilation of a list of potential Douglas fir forest stands, from which 20 were progressively selected and sampled during the summer of 1965. These stands were selected in the field by reference to a list of selection criteria intended to ensure that they
   1) were free of major human disturbance;
   2) were of adequate sampling area and had at least 50% Douglas fir by subjective volume estimate;
   3) were free of disturbance due to disease, fire and lumbering;
   4) were reasonably uniform in topography,

aspect and slope angle.

Subsequently, one stand in Waterton National Park was sampled for comparison purposes.

3. Restricted random sampling methods were used to sample the stands to a density of one random point per 8000 square feet. At each random point nested square quadrats were set up to quantitatively sample attributes of the vegetation strata; 10 x 10 meter quadrats for trees, tall shrubs and saplings, 4 x 4 meter quadrats for shrubs and transgressives and 1 x 1 meter quadrats for herbs, dwarf shrubs, tree seedlings, bryophytes and lichens. The stand area was sampled sequentially until a previously-fixed minimum standard error was obtained equivalent to 10% of the mean density of all trees, and also to 15% of the mean density of Douglas fir.

4. As a result of quadrat sampling and certain observations made inside the stand area as a whole, estimates were obtained of the following compositional, populational and structural attributes of the vegetation: Presence, quadrat Frequency and cover of all vascular species, terrestrial bryophytes and lichens, density of species in the tree and shrub strata, basal area and DBH of tree species, the age,

height and DBH of selected trees, point-to-tree distances to the nearest Douglas fir, and light intensity readings at preselected intervals through the stand.

5. Observations were made on slope angle, slope aspect, elevation, soil and air temperatures. Soil horizon samples were analyzed for composition, texture, moisture characteristics and available mineral nutrients.

6. Of 140 vascular species recorded, only 15 had Presence values over 80% and only 12 had mean quadrat Frequencies over 20%, indicating that the large majority of species have either a very scattered or a limited distribution.

7. Two tree species, blue Douglas fir and lodgepole pine made up the bulk of the 45% mean cover of the tree stratum and were present in all stands. The only other common tree species, white spruce and aspen, were of limited distribution and only local importance. The average basal area estimates of the four tree species were 111.7 for Douglas fir, 16.1 for lodgepole pine, 4.7 for white spruce and 0.8 for aspen in square feet per acre.

8. The prevailing height of the tree stratum in all stands was very largely a function of the more mature Douglas fir. There were indications that:

   1) the tree canopy becomes increasingly irregular with increasing height and age;
   2) lodgepole pine and aspen being overtopped and competitively eliminated by Douglas fir.

9. The maximum ages of Douglas fir in stands varied between 76 and 367 years. The younger stands were even-aged and indicative of extensive fires in the Banff area from 1880 - 1890. The trees in most of the older stands were divisible into two or more age groups, possibly originating after successive fires which destroyed all but the thick-barked older fir.

10. There was progressive decrease in density with increase in size for all four tree species, although saplings, transgressives and seedlings were all of lower density than the trees. Reproductive stages of all four tree species were poorly represented in the mature phase of this ecosystem, although those of Douglas fir had by far the highest Frequency. There was evidence to support the hypothesis that the critical period occurs before the transgressive stage of the life cycle, and that large-scale thinning out

does not often occur thereafter. Density of dead aspen exceeded that of live aspen, probably due to heavy browsing by ungulates.

11. Most stands could be classified into four diameter-class, distribution types which possibly represent different stages in a maturation cycle of Douglas fir. Fir becomes increasingly important with age, until over-maturity results in canopy openings, which then support patches of mixed tree species reproduction.

12. Two methods of assessing the dispersion pattern of the tree stratum were used:

1) based on the coefficient of dispersion (Blackman, 1942);

2) based on random point-to-nearest tree distance measures (Pielou, 1959).

The two methods showed poor agreement regarding the degree of aggregation of Douglas fir stands, possibly due to the different emphasis placed on the scale of pattern by the two methods. Lodgepole pine and white spruce nearly always tended to be aggregated. There was evidence that pine (and perhaps fir and spruce) tends to be clumped in canopy openings in its younger reproductive stages but more and more randomly dis-

persed with increasing age due to inter- and intra-specific competition.

13. The mean cover of the poorly-developed shrub stratum was only 6%. The four principal species were *Shepherdia canadensis*, *Rosa acicularis*, *Spiraea lucida* and *Juniperus communis*; *Shepherdia* having a mean height of about 2½ feet and all the other shrub species form a lower layer at a height of 6 - 18 inches.

14. The mean cover of the herb and dwarf shrub stratum was 30%; the grass *Elymus innovatus* and the dwarf shrub *Arctostaphylos uva-ursi* were responsible for well over half of the total stratum cover in Jasper stands; together with the grass *Calamagrostis rubescens*, they accounted for a similarly large fraction at Banff. The only other herb and dwarf shrub species of significant prominence were *Linnaea borealis*, *Aster conspicuus*, *Astragalus decumbens* and *Fragaria virginiana*.

15. *Calamagrostis* was the principal member in a group of differential species to the Banff area; no such differential grouping was present at Jasper.

16. The mean cover of terrestrial bryophytes was 10%, most of which was attributable to *Hylocomium splendens*. The only other prominent bryophytes were *Abietinella abietina*, often associated with *Hylocomium* in feather moss carpets, and *Tortula ruralis* on dry mineral soil and needle litter.

17. The mean cover of terrestrial lichens was 5%, most of which was attributable to species of *Peltigera*, the most frequent of which was *P. canina* var. *rufescens*, on exposed south-facing slopes. Many unidentified species of *Cladonia* were also very frequent.

18. The mean elevation of Banff stands was approximately 1300 feet higher than that of Jasper stands. Most stands in both parks were situated either on level terraces, ridges, or on south-facing slopes of varying steepness and uniformity.

19. Soil profiles in Banff and Jasper were poorly-developed and topped by a clearly differentiated but thin humus horizon. These profiles have usually developed on well-drained glacial tills or outwash, less commonly on bedrock, and composed predominantly of limestone and dolomite at Banff and quartzite sandstones and conglomerates at Jasper.

20. The Banff soil profiles have caliche deposits at varying depths, and were generally alkaline, whereas Jasper soil profiles were neutral to acid.

21. Most soils were classified either as loams or sandy loams, and were very deficient in available nitrogen and phosphorus. There was no marked deficiency of available potassium. The water availability values of soil profiles varied from a low of 3% in loamy sand to a high of 23% in silty loam, and showed little correlation with soil texture except for unusually sandy soils.

22. Multiple regression was used to relate the vegetation to the environment on a quantitative basis, as the method of simple correlation gives only a partial measure of association between pairs of variables and is therefore inadequate to obtain an understanding of the control of vegetation by environment. Multiple regression equations were computed for 14 attributes of vegetation structure and population size, using independent variables selected from the environmental data collected in this study, and appropriate to the dependent variable.

23. The most influential independent variables in

equations of tree stratum attributes were aspect, available phosphorus, available potassium at 10 inches soil depth, and effective stand age. The first three seem to be important factors limiting to the development of the Douglas fir ecosystem.

24. The subordinate strata were strongly but differentially dependent on variables associated with the tree canopy, less so on topography, and much less so on edaphic variables. The proportion of lodgepole pine in the tree canopy is strongly correlated with the cover of the herb and dwarf shrub stratum. It is hypothesized that this correlation is due to the relatively thin and diffuse canopy afforded by pine, allowing improved light intensity and water availability to the subordinate strata.

25. To investigate the relations between stands treated as vegetation units, a two-dimensional ordination was constructed based on an index of similarity between stands. This index, based on similarity of floristic composition and population size, enabled a placement of stands on the ordination field such that distances between stands were inversely proportional to their similarity. This ordination then provided a framework on which quantitative data were plotted to

detect association between species or correlations between species populations and environmental variables. The ordination field used for these purposes did not include the Waterton stand due to its extreme dissimilarity from the 20 Banff and Jasper stands.

26. A clear division was found between the stands of Banff and Jasper on the ordination field; most Banff stands were spread over the upper left quadrant, whereas most Jasper stands were clustered at the right side of the field.

27. Total tree cover, Douglas fir basal area, height and effective stand age were all at a maximum in the right-center field, whereas lodgepole pine basal area was at a maximum in the upper left quadrant. The standing crop total basal area was fairly uniform in distribution, but the relative amounts contributed by pine and fir differed according to stand age. Older, taller, heavier-canopied stands of fir were mostly situated at Jasper. As the ordination was constructed on attributes of the understory, it has been inferred that changes in its composition and abundance are paralleled closely and probably regulated by changes in the tree canopy.

28. Three of the four major shrub species (*Rosa acicularis*, *Shepherdia canadensis* and *Spiraea lucida*) were positively associated but had poorly-defined ordination patterns. However, *Juniperus communis*, together with *J. horizontalis* and *Rosa woodsii*, formed a well-defined species group in the left-centre of the field, associated with young and light-canopied stands. These shrubs seemed to represent a trend from *Rosa acicularis* with high Frequency and wide environmental tolerance to *Juniperus communis* with relatively low Frequency and a restricted distribution due to a narrow tolerance range.

29. Six herb and dwarf shrub species, of which the most prominent was *Arctostaphylos uva-ursi*, formed a closely-associated group with populational maxima in that part of the field characterized by a high proportion of pine in young, light-canopied stands (Banff stands of left and upper center). *Calamagrostis rubescens* was restricted to the upper center part of the field and, together with many other less prominent species, was restricted almost entirely to Banff stands. *Elymus innovatus* showed a maximum Frequency in the Jasper part of the field and appeared to have a greater tolerance to shading than most of its competitors in the understory.

30. *Hylocomium splendens*, the most prominent constituent of the feather moss carpets, reached maximum population size in the right-center of the field, in stands characterized by high tree cover. This correlation may reflect an ability to tolerate low light intensity and/or a sensitivity to extremes of temperature and moisture. A strong positive association was indicated between *Tortula ruralis* and available phosphorus in the soil.

31. Only six quantitative environmental variables showed clearly-defined patterns on the ordination: elevation, field capacity, permanent wilting percentage, free lime and hydrogen ion concentration in the mineral soil. The latter two variables peaked in the Banff part of the field as expected from the type of bedrock or substratum. Higher field capacity and permanent wilting percentage of the soil in the Banff part of the ordination field may offset the higher precipitation (especially in spring) at Banff and result in similar soil moisture conditions for the Douglas fir vegetation of both parks.

32. At least six sets of environmental factors were associated with the floristic discontinuity between Banff and Jasper, namely elevation, climate, moisture characteristics and lime content of the soil, the proportion of pine in the canopy and structural attributes

of the tree canopy pertaining to stand history. It is thought likely that this floristic discontinuity is primarily a consequence of local stand history, although climate and edaphic differences probably have influence on individual species distributions and population sizes.

33. Two associations were recognized, based on the floristic discontinuity:

1) the *Pseudotsuga menziesii/Elymus innovatus* association of Jasper;
2) the *Pseudotsuga menziesii/Arctostaphylos uva-ursi - Calamagrostis rubescens* association of Banff.

These two associations could represent different stages in a maturation cycle of Douglas fir forest, and/or be a result of environmental factors influencing the distribution and competitive ability of individual understory species.

34. This ecosystem has been compared with, and found similar to other Douglas fir forests in British Columbia and the northern Rocky Mountains and it can be looked upon as a modification of the Douglas fir zone in southern British Columbia which has extended through passes in the Rocky Mountains.

35. The primary producer level of the Douglas fir ecosystem at Banff and Jasper has been considerably altered during the last century by several factors attributable to man's influence. Chief among these factors are:

1) fire, which has resulted in the replacement of Douglas fir forests by seral species such as lodgepole pine and aspen;
2) over-grazing and browsing by ungulates, especially elk which has had an adverse effect on tree regeneration and impoverished the understory vegetation, notably the shrub stratum.

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APPENDIX 1. LOCATIONS OF STANDS AND SAMPLING DATES

Stand	Date Sampled 1965	Latitude (North) Degrees	Mins.	Longitude (West) Degrees	Mins.	Mean Elevation (feet)	Mean Aspect	Mean Slope (degrees)
1B	June 10-12	51	11	115	33	4600	S33E	9
2B	June 14-16	51	12½	115	33½	4800	S 7E	20
3J	June 18-20	52	54½	118	2	3390	Nil	Nil
4J	June 21-22	52	55	118	2	3560	S36E	7
5J	June 23-24	52	54	118	3	3675	S49E	13
6J	June 25 & July 17-18	53	9½	118	2	3590	S36W	3
7B	June 27-28	51	11½	115	35	5520	S19W	25
8B	June 30 - July 1	51	10	115	26½	4670	S39W	5
9B	July 8-9	51	11	115	36	4730	S 6W	23
10B	July 11-12	51	14	115	29½	5050	S19E	15
11B	July 13-14	51	10	115	26½	4660	Nil	Nil
12J	July 19-20	53	2½	118	12½	3480	N58E	4
13J	July 22-24	52	53	118	20	3670	S13W	26
14J	July 25-26	52	53½	118	23½	3920	S 5W	13
15J	July 27-29	52	48½	118	1	3720	N30W	10
16J	August 3-5	52	56	118	2½	3840	N65W	10
17J	August 6-8	52	56	118	3	4000	S52E	18
18J	August 9-11	52	49	118	1	3700	S36W	16
19B	August 14-15	51	8	115	24	4600	S20W	7
20B	August 16-17	51	10½	115	29½	4620	S 1E	17
21W	August 20-21	49	4	113	57	4870	S35W	15

APPENDIX 2. AERIAL PHOTOGRAPHS OF STUDY AREAS IN BANFF AND JASPER NATIONAL PARKS

The following aerial photographs (1:40,000) were used to locate stands during the preliminary study. (Obtainable from the Department of Lands and Forests, Natural Resources Building, Edmonton)

Section Number	Series Number	Flight Line	Photograph Number
82-0-4	160	5106X	21
82-0-4 and 82-0-3	160	5104X	16 - 18
83-D-16	160	5218X	11
83-D-16	160	5220X	6
83-D-16	160	5221X	15
83-E-1	160	5301X	17
83-E-1	160	5304X	20

APPENDIX 3. INDICES OF SIMILARITY BETWEEN STANDS

Using prominence values of 151 vascular species (see pages 112-117).

ST	21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2
1	7.7	63.2	51.1	27.9	26.8	39.4	20.8	16.9	22.1	17.3	41.4	27.0	49.6	47.0	19.7	36.3	20.0	23.7	41.9	63.1
2	9.7	67.3	44.8	20.5	18.6	42.2	17.1	19.0	23.0	13.5	42.5	19.7	39.0	47.2	13.0	33.4	12.8	17.1	30.9	
3	5.7	39.1	45.0	57.7	60.9	38.4	32.5	53.7	53.1	53.7	45.1	45.9	30.9	37.6	51.2	65.4	69.5	69.2		
4	10.5	23.1	29.8	62.0	71.7	26.9	34.6	65.5	60.3	62.8	31.6	40.5	25.5	25.3	62.9	57.2	83.2			
5	5.8	20.7	27.0	62.2	70.4	19.9	37.5	63.2	58.1	60.9	29.8	39.3	22.3	21.4	59.2	51.0				
6	16.8	38.6	42.3	55.1	55.8	54.7	40.0	62.5	69.1	54.3	43.4	44.0	30.1	38.9	44.2					
7	14.3	33.4	45.6	38.7	51.9	20.3	22.5	57.7	42.3	46.5	46.4	56.4	30.9	40.1						
8	5.9	66.3	69.9	29.0	26.3	41.1	25.0	25.9	31.2	27.7	74.6	46.3	32.2							
9	8.8	49.3	39.5	35.9	30.3	30.9	23.6	19.3	24.3	14.8	27.0	38.2								
10	9.9	39.7	52.9	42.6	49.2	26.4	22.5	37.1	42.8	33.4	64.8									
11	7.4	59.1	65.3	29.8	35.8	39.6	19.9	33.4	39.6	36.5										
12	9.1	17.0	24.7	45.0	55.8	42.1	38.3	60.7	63.3											
13	11.6	29.7	35.7	62.0	65.0	49.0	50.6	67.5												
14	19.8	25.0	26.8	47.2	54.7	39.3	36.0													
15	6.2	23.2	23.6	49.9	41.7	34.9														
16	14.7	43.5	41.3	30.4	27.8															
17	10.8	26.7	36.1	69.0																
18	10.2	30.2	36.1																	
19	9.1	67.4																		
20	11.2																			

APPENDIX 4. VASCULAR FLORA OF THE DOUGLAS FIR STANDS IN BANFF, JASPER AND WATERTON NATIONAL PARKS

Species listed in the order found in E.H. Moss' "Flora of Alberta" (1959).

"X" denotes species recorded only from Waterton National Park.

Polypodiaceae

Cystopteris fragilis (L.) Bernh.

X *Polypodium vulgare* var. *columbianum* Gilbert

Lycopodiaceae

Selaginella densa Rydb.

Pinaceae

X *Abies lasiocarpa* (Hook.) Nutt.

Juniperus communis L.

Juniperus horizontalis Moench

Picea glauca (Moench) Voss

Pinus contorta Loudon var. *latifolia* Engelm.

Pseudotsuga menziesii var. *glauca* (Beissn.) Franco

Gramineae

Agropyron dasystachyum (Hook.) Scribn.

APPENDIX 4. (continued)

Gramineae (continued)

Agropyron griffithsii Scribn. & Smith

Agropyron spicatum (Pursh) Scribn. & Smith

Agropyron subsecundum (Link) Hitchc.

Bromus pumpellianus Scribn.

X *Bromus vulgaris* (Hook.) Shear

Calamagrostis purpurascens R. Br.

Calamagrostis rubescens Buckl.

Danthonia intermedia Vasey

X *Elymus glaucus* Buckl.

Elymus innovatus Beal

X *Festuca occidentalis* Hook.

Festuca saximontana Rydb.

Festuca scabrella Torr.

Koeleria cristata (L.) Pers.

Phleum pratense L.

Poa interior Rydb.

Poa palustris L. (?)

Poa pratensis L. (?)

Poa sp.

Stipa columbiana Macoun

Stipa richardsonii Link

Trisetum spicatum (L.) Richt.

APPENDIX 4. (continued)

Cyperaceae

Carex concinna R. Br.

Carex concinnoides Mack.

X *Carex geyeri* Boott

Carex richardsonii R. Br.

Carex umbellata Schk.

Kobresia simpliciuscula (Wahlenb.) Mack.

Liliaceae

Allium cernuum Roth.

X *Clintonia uniflora* (Schult.) Kunth

Disporum trachycarpum (S. Wats.) B. & H.

Lilium philadelphicum L. var. *andinum* (Nutt.) Ker

Smilacina racemosa (L.) Desf. var. *amplexicaulis* (Nutt.) S. Wats.

Stenanthium occidentale A. Gray

X *Veratrum eschscholtzii* A. Gray

X *Xerophyllum tenax* (Pursh) Nutt.

Zygadenus elegans Pursh

Zygadenus gramineus Rydb.

Iridaceae

Sisyrinchium montanum Greene

APPENDIX 4. (continued)

Orchidaceae

Calypso bulbosa (L.) Oakes

Corallorhiza trifida Chatelâin

X *Goodyera oblongifolia* Raf.

Goodyera repens (L.) R. Br.

Habenaria viridis (L.) R. Br. var. *bracteata* (Muhl.) A. Gray

Salicaceae

Populus balsamifera L.

Populus tremuloides Michx.

Salix spp. (2)

Betulaceae

Betula papyrifera Marsh.

Santalaceae

Comandra pallida A. DC.

Geocaulon lividum (Richards.) Fern.

Loranthaceae

Arceuthobium americanum Nutt.

APPENDIX 4. (continued)

Chenopodiaceae

Chenopodium album L.

Chenopodium capitatum (L.) Aschers.

Caryophyllaceae

Arenaria lateriflora L.

Cerastium arvense L.

Stellaria longipes Goldie

Ranunculaceae

Actaea rubra (Ait.) Willd.

Anemone multifida Poir.

Anemone patens L. var. *Wolfgangiana* (Bess.) Koch

X *Aquilegia brevistyla* Hook. (?)

Clematis verticellaris DC. var. *columbiana* (Nutt.) A. Gray

Thalictrum occidentale A. Gray (?)

Berberidaceae

X *Mahonia repens* (Lindl.) G. Don.

Cruciferae

Arabis hirsuta (L.) Scop. var. *pycnocarpa* (Hopkins) Rollins

APPENDIX 4. (continued)

Cruciferae (continued)

Arabis holboellii Hornem. var. *retrofracta* (Graham) Rydb.

Draba aurea Vahl. (?)

Erysimum inconspicuum (S. Wats.) MacM.

Crassulaceae

Sedum stenopetalum Pursh.

Saxifragaceae

Heuchera cylindrica Dougl.

Ribes glandulosum Grauer

Ribes oxyacanthoides L.

Saxifraga bronchialis L.

Saxifraga tricuspidata Rottb.

Rosaceae

Amelanchier alnifolia Nutt.

Fragaria virginiana Duchesne var. *glauca* S. Wats.

Geum triflorum Pursh

Potentilla fruticosa L.

Potentilla pensylvanica L.

Potentilla sp.

APPENDIX 4. (continued)

Rosaceae (continued)

Rosa acicularis Lindl.

Rosa woodsii Lindl.

X *Rubus parviflorus* Nutt.

X *Rubus strigosus* Michx.

Spiraea lucida Dougl.

Leguminosae

Astragalus decumbens (Nutt.) A. Gray var. *serotinus* (Gray) M.E. Jones

Astragalus striatus Nutt.

Hedysarum alpinum L.

Hedysarum mackenzii Richards.

Hedysarum sulphurescens Rydb.

Lathyrus ochroleucus Hook.

Oxytropis campestris (L.) DC.

Oxytropis deflexa (Pall.) DC.

Oxytropis sericea Nutt. var. *spicata* (Hook.) Barneby

Oxytropis splendens Dougl.

Vicia americana Muhl.

Linaceae

Linum lewisii Pursh

APPENDIX 4. (continued)

Aceraceae

X *Acer glabrum* Torr.

Violaceae

Viola adunca J.E. Smith

Viola rugulosa Greene

Elaeagnaceae

Elaeagnus commutata Bernh.

Shepherdia canadensis (L.) Nutt.

Onagraceae

Epilobium angustifolium L.

Umbelliferae

Lomatium simplex (Nutt.) MacBr. var. *leptophyllum* (Hook.) Mathias

Osmorhiza chilensis Hook. & Arn.

Osmorhiza depauperata Philippi

Cornaceae

Cornus canadensis L.

APPENDIX 4. (continued)

Cornaceae (continued)

X *Cornus stolonifera* Michx.

Pyrolaceae

X *Chimaphila umbellata* (L.) Bart. var. *occidentalis* (Rydb.) Blake

Pyrola secunda L.

Pyrola virens Schweigg.

Ericaceae

Arctostaphylos uva-ursi (L.) Spreng.

Vaccinium caespitosum Michx.

Primulaceae

Androsace septentrionalis L.

Dodecatheon conjugens Greene

Gentianaceae

Gentianella amarella (L.) Borner ssp. *acuta* (Michx.) J.M. Gillett

APPENDIX 4. (continued)

Apocynaceae

Apocynum androsaemifolium L.

Labiatae

X *Monarda fistulosa* L. var. *menthaefolia* (Graham) Fern.

Scrophulariaceae

Castilleja miniata Dougl.

Collinsia parviflora Dougl.

Orthocarpus luteus Nutt.

Penstemon confertus Dougl.

Rubiaceae

Galium boreale L.

Galium triflorum Michx.

Caprifoliaceae

Linnaea borealis L. var. *americana* (Forbes) Rehd.

Lonicera dioica L. var. *glaucescens* (Rydb.) Butters

Symphoricarpos occidentalis Hook.

Viburnum trilobum Marsh.

APPENDIX 4. (continued)

Campanulaceae

Campanula rotundifolia L.

Compositae

Achillea millefolium L.

Agoseris glauca (Pursh) Raf.

Antennaria neglecta Greene

Antennaria nitida Greene

Antennaria racemosa Hook.

Antennaria rosea Greene

Arnica cordifolia Hook.

Artemisia campestris L.

Artemisia frigida Willd.

Aster alpinus L.

Aster ciliolatus Lindl.

Aster conspicuus Lindl.

Aster laevis L. var. *geyeri* A. Gray

Aster sibiricus L.

X *Balsamorhiza sagittata* (Pursh) Nutt.

Chrysanthemum leucanthemum L.

Chrysopsis villosa (Pursh) Nutt.

Crepis atrabarba Heller

Erigeron caespitosus Nutt.

APPENDIX 4. (continued)

Compositae (continued)

Erigeron compositus Pursh var. *glabratus* Macoun

Erigeron glabellus Nutt.

Gaillardia aristata Pursh

Hieracium albiflorum Hook.

Hieracium canadense Michx.

Senecio canus Hook.

Senecio cymbalarioides Nutt.

Senecio pseudaureus Rydb. (?)

Solidago decumbens Greene

Taraxacum sp.

APPENDIX 5. TERRESTRIAL BRYOPHYTE AND LICHEN FLORA OF THE DOUGLAS FIR STANDS IN BANFF, JASPER AND WATERTON NATIONAL PARKS

"X" denotes species recorded only from Waterton National Park.

MOSSES: Species listed in the order found in Bird (1964)

Ditrichaceae

Ceratodon purpureus (Hedw.) Brid.

Ditrichum flexicaule (Schwaegr.) Hamp.

Dicranaceae

Dicranum fragilifolium Lindb.

Dicranum fuscescens Turn.

Dicranum rugosum (Hoffm.) Brid.

X *Dicranum scoparium* Hedw.

Pottiaceae

Tortella tortuosa (Hedw.) Limpr.

Tortula ruralis (Hedw.) Crom.

Grimmiaceae

Schistidium alpicola (Hedw.) Limpr.

APPENDIX 5. (continued)

MOSSES (continued)

Bryaceae

Pohlia nutans (Hedw.) Lindb.

Mniaceae

X *Mnium lycopodioides* Schwaegr.

X *Mnium spinulosum* B.S.G.

Timmiaceae

Timmia austriaca Hedw.

Orthotrichaceae

Orthotrichum macounii Aust.

Hedwigiaceae

Hedwigia ciliata (Hedw.) P. Beauv.

Leskeaceae

X *Lescuraea radicosa* (Mitt.) Moenk.

APPENDIX 5. (continued)

MOSSES (continued)

Thuidiaceae

Abietinella abietina (Hedw.) Fleisch.

Amblystegiaceae

Drepanocladus uncinatus (Hedw.) Warnst.

Brachytheciaceae

Brachythecium salebrosum (Weg. and Mohr) B.S.G.

X *Camptothecium aureum* (Lag.) B.S.G.

Eurhynchium pulchellum (Hedw.) Jenn.

Entodontaceae

Pleurozium schreberi (Brid.) Mitt.

Hypnaceae

Hypnum revolutum (Mitt.) Lindb.

Ptilium crista-castrensis (Hedw.) De Not.

Pylaisia polyantha B.S.G.

APPENDIX 5. (continued)

MOSSES (continued)

Rhytidiaceae

Rhytidiadelphus triquetrus (Hedw.) Warnst.

Rhytidium rugosum (Hedw.) Kindb.

Hylocomiaceae

Hylocomium splendens (Hedw.) B.S.G.

Polytrichaceae

Polytrichum juniperinum Hedw.

LIVERWORTS: Species listed in the order found in Schuster (1958)

Lophoziaceae

Barbilophozia hatcheri (Evs.) Steph.

Lophocoleaceae

Lophocolea minor Nees

APPENDIX 5. (continued)

LIVERWORTS (continued)

Ptilidiaceae

Ptilidium ciliare (L.) Nees

Ptilidium pulcherrimum (Web.) Hampe

LICHENS: Species listed in the order found in Bird (1966)

Cladoniaceae

Cladonia spp.

Collemataceae

Leptogium saturninum (Dicks.) Nyl.

Parmeliaceae

Cetraria cucullata (Bell.) Ach.

Cetraria glauca (L.) Ach.

Cetraria islandica (L.) Ach.

Cetraria nivalis (L.) Ach.

Cetraria pinastri (Scop.) S. Gray

Parmelia conspersa (Ach.) Ach.

Parmelia enteromorpha Ach.

Parmelia physodes (L.) Ach.

APPENDIX 5. (continued)

LICHENS (continued)

Parmeliaceae (continued)

Parmelia sulcata Tayl.

Peltigeraceae

Peltigera aphthosa (L.) Willd.

Peltigera aphthosa var. *variolosa* (Mass.) Thoms.

Peltigera canina (L.) Willd.

Peltigera canina var. *rufescens* (Weis.) Mudd

Peltigera horizontalis (Huds.) Baumg.

Peltigera polydactyla (Neck.) Hoffm.

Physciaceae

Physcia sp.

Stereocaulaceae

Stereocaulon tomentosum Fr.

Stictaceae

Lobaria pulmonaria (L.) Hoffm.

APPENDIX 5. (continued)

LICHENS (continued)

Usneaceae

Alectoria spp.

Letharia vulpina (L.) Vain.

Usnea spp.

APPENDIX 6. NOTES ON THE CONSTRUCTION OF MULTIPLE REGRESSION EQUATIONS

Using library program G2011, Department of Computing Science, University of Alberta, Edmonton.

The total number of independent variables that could be used in regression program No. G2011 was 49 and it was apparent that the total number of transformed and the untransformed variables would exceed the limit for regressions involving Y_5 to Y_{14} inclusive. For example, the total possible, appropriate variables for the regression of Y_{14} would be 59. Therefore, it was necessary to complete regressions Y_5 to Y_{14} in two stages as follows. For the first stage, the untransformed variables were used together with the transformations of the form X^2, $\log_{10}X$, cosine X and sine X. For the second stage the untransformed variables were used together with the transformations of the form X^3 and all the transformations of the form X^2, $\log_{10}X$, cosine X and sine X that appeared in the first stage regression equation, to give the final regression equation.

A restriction was imposed on the number of terms in the regression equation such that the number of sets of observations must be greater than the number of regression coefficients to be estimated. As it was only intended to use data from 20 stands, the number of independent variables

APPENDIX 6. (continued)

to feature in the final equation was limited to less than 20. The reason for this limitation was that a perfect fit to a set of 20 observations would be obtained with 19 terms in the regression equation.

However, in these regression analyses the number of independent variables fed into the program greatly exceeded 19 so that some way had to be found to terminate the equation well before this perfect fit had been reached. Therefore, an arbitrary cut-off point was established after the first eight terms in the equation, unless an optimal fit was obtained before this cut-off point (if the addition of any terms failed to reduce significantly the residual variation.

A typical multiple regression equation might have the following form:

$$Y_1 = A + B_1X_{12} - B_2X_2^2 + B_3X_8 + B_4X_{12}^3 - B_5X_6^2 + B_6 \log_{10}X_2 + B_7 \log_{10}X_{12} - B_8X_7^3$$

The first independent variable (X_{12}) was then the variable that accounted for the greatest amount of the variation in the dependent variable (Y_1) of the list of variables entered in the program. The second variable (X_2^2) accounted for the greatest amount of the residual variation

APPENDIX 6. (continued)

after the effect of the variable X_{12} had been removed. This is equivalent to saying that the variation due to X_{12} had been held constant. The regression coefficients (B_1, B_2, etc.) and the equation constant (A) were for the complete equation of eight terms and not for a larger equation reported in abbreviated form.

APPENDIX 7. DETAILS OF THE METHOD OF DETERMINING CANOPY COVER FROM VERTICAL PHOTOGRAPHS

Some method of point sampling of the photographic print was preferred to the alternative methods of area tracing with a planimeter or subjective estimates. Diffuse foliage would be very difficult to trace accurately. Quantitative methods would enable results to be used in analyses requiring objective data, and so minimize the personal bias always inherent in subjective estimates.

The prints were sampled as follows: First, the sampling area in the print was reduced to that of a circle with diameter equivalent to the width of the print (5.6 cm), and with center at the print's center point. This tended to eliminate most of the distortion evident at the ends of the rectangle. Then four concentric circles of radii 1.40, 1.98, 2.42 and 2.80 cm were drawn on a transparent overlay of the 5.6 cm x 8.4 cm print (Fig. 6, p. 57).

It was not necessary to position the sampling points randomly on the overlay; instead they were positioned equidistant from each other insofar as was possible within the limits imposed by the circles. Each consecutively larger circle was sampled proportionately to area; the innermost circle enclosed 10 points, the second circle 20 points, the third 30 and the outermost circle 40. This overlay was superimposed on each print in turn and the

APPENDIX 7. (continued)

presence or absence of tree cover under each point recorded. The estimated mean tree cover for the stand was taken to be the number of points covering foliage as a percentage of the total possible for all photographs.

It was found that the mean cover tended to increase as the radius of the circle increased (Fig. 7, p. 57). However no constant relationship was apparent between the results obtained from the concentric circles. In some stands the graphical representation was parallel with the X axis; in others the graph formed a wide angle with the X axis. It was generally found that the larger the radius, the greater was the distortion due to the field of view including more and more lateral vegetation. For example, tree trunks on the edge of the photograph appeared to curve into the center, and, therefore, occupied a disportionately large area of the photograph. Consequently, it was thought that the smaller the center-based sampling area, the more accurate would be the cover estimate. Taken to an extreme, the only absolutely accurate result would be that obtained by sampling the centre point alone. Only one sample point per photograph would result in too high a margin of error due to too few points.

It was thought that the solution to this problem might have been to subtend to the 'percentage cover' axis,

APPENDIX 7. (continued)

the line obtained from plotting the percentage cover against the relative area of the circle (Fig. 7, p. 57). The value registered on the 'percentage cover' axis would represent the cover obtained by sampling an infinitely small area in the center of the photograph, the center point. However, as some graphs were parallel with, and others were at a wide angle to the X axis, a satisfactory method of subtending these lines was never found. Subtending the sloping graphs to the axis produced highly distorted results that were obviously far too low. Eventually it was decided that the smallest error factor would be obtained from the sampling data of the innermost circle. These values would still be a little higher than the actual cover, but the potential error would be much less than that of the subjective field estimates, and comparable from stand to stand.

Further study of this technique would undoubtedly produce a standard formula devised to compensate for the factors producing distortion and errors inherent in this method; compensate for differing camera angles, height of tree stratum and slope of ground.

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